











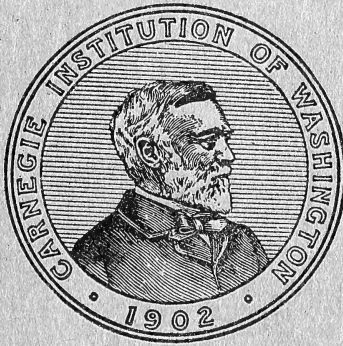
Francis G. Benedict *H. M. Mann*

# THE PHYSIOLOGY OF LARGE REPTILES

WITH SPECIAL REFERENCE TO THE  
HEAT PRODUCTION OF SNAKES, TORTOISES,  
LIZARDS AND ALLIGATORS

By FRANCIS G. BENEDICT

*Director, Nutrition Laboratory, Carnegie Institution of Washington*



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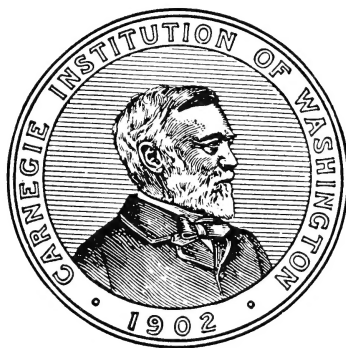
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# THE PHYSIOLOGY OF LARGE REPTILES

## INTRODUCTION

This report, which deals not simply with the gaseous metabolism but to a considerable extent with the physiology in general of many of the large poikilotherms, touches upon a field of research that has already attracted many workers. Owing to the rapid advances made in the technique for studying animals of this type in the last two decades and especially to the existence of several excellent general articles on this subject, it will be unnecessary to extend the limits of this report to give (as is customary in Nutrition Laboratory monographs) an extensive bibliography. So far as the early literature is concerned, the article of Zuntz<sup>1</sup> in Hermann's Handbuch, prepared with the meticulous care used in all his writings, is of special interest, as evidenced by the fact that since its publication it has been the basis of practically all discussions by subsequent writers on gaseous metabolism. Among the later collections of literature dealing with the gaseous exchange of cold-blooded animals is the review by Tigerstedt<sup>2</sup> in Winterstein's Handbuch, which is accompanied by a number of keen comments born of his own experience, the extensive compilation by Kestner and Plaut,<sup>3</sup> likewise in Winterstein's Handbuch, and the article by Cronheim<sup>4</sup> in Oppenheimer's Handbuch, which covers much the same ground as the report by Kestner and Plaut but includes later literature. Detailed consideration of the metabolism of cold-blooded animals, although only a part of his main treatment, is incorporated in Krogh's excellent monograph on the respiratory exchange of animals and man.<sup>5</sup> The outstanding individual researches of present-day value on poikilotherms are undoubtedly those of Krehl and Soetbeer,<sup>6</sup> Krogh<sup>7</sup> and Rubner.<sup>8</sup> Rubner's interest in the metabolism of cold-blooded animals dates back many years, and he has continually recognized in numerous papers the important rôle that cold-blooded animals play in studies dealing with general physiology. His two articles published in 1924 represent a most complete summarization of the results of his studies covering several decades. No publications have been more stimulating and of greater value to the Nutrition Laboratory, particularly in the preparation and analysis of our results, than have these two fundamental papers of Rubner. In citing these striking contributions of Rubner, Krogh, and Krehl and Soetbeer, it is not meant to underestimate the contributions made by others, and the frequent literature citations throughout this report will show that the papers of Hill, Vernon, Martin, Regnault and Reiset, Hári and others have been of incalculable service in this present research.

<sup>1</sup> Zuntz, N., Hermann's Handb. d. Physiol., 1882, **4** (Pt. 2), pp. 145 *et seq.*

<sup>2</sup> Tigerstedt, R., Winterstein's Handb. d. vergl. Physiol., 1910-1914, **3** (Pt. 2), p. 1.

<sup>3</sup> Kestner, O., and R. Plaut, Winterstein's Handb. d. vergl. Physiol., 1924, **2** (Pt. 2), p. 901.

<sup>4</sup> Cronheim, W., Oppenheimer's Handb. d. Biochem., 1927, 2d ed., **7**, p. 291.

<sup>5</sup> Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, 173 pp.

<sup>6</sup> Krehl, L., and F. Soetbeer, Arch. f. d. ges. Physiol., 1899, **77**, p. 611.

<sup>7</sup> Ege, R., and A. Krogh, Internat. Revue f. Hydrobiol., 1914, **6**, p. 48; Krogh, A., Internat. Zeitschr. f. physik.-chem. Biol., 1914, **1**, p. 491.

<sup>8</sup> Rubner, M., Biochem. Zeitschr., 1924, **148**, pp. 222 and 268.



Comparative physiology is most helpful in illuminating the many problems in human physiology. Particularly is this true in studying the laws governing heat production and heat loss, the balance between thermogenesis and thermolysis, the physiological heat regulation, the body temperature, the reaction of the living organism to environmental temperature, and the mobility of the protoplasm at different temperatures. Physiologists turn to studies in comparative physiology in the search for interpretation of phenomena in human physiology. The Nutrition Laboratory has had a comprehensive program for studying the comparative physiology of animals, with special reference to the gaseous metabolism. Thus far its observations have dealt with animals ranging in size from the 150-gram dove and the small albino rat to the 600-kg. cow, steer and horse. Information concerning the physiology of each of these animals may be said to contribute directly toward our knowledge of the physiology of humans. It is believed that much the same can be said with regard to a study of the physiology of the cold-blooded animals, particularly a study of their various methods of heat production, heat loss and water loss, the character of their katabolism, and their reaction to temperature, both internal and external, with special reference to the comparison of the protoplasmic activity of warm-blooded and cold-blooded animals as measured by their oxygen consumption or carbon-dioxide production at or about 37° C., that is, the ordinary body temperature of warm-blooded animals. Indeed, physicians have had these comparisons in mind, for Krehl and Soetbeer<sup>1</sup> state in their classic research that, in searching for the origin of the increase in heat production during fever, they found it necessary to study the heat economy of cold-blooded vertebrates. The factors entering into the heat loss of cold-blooded animals differ to such an extent from the factors influencing the heat loss of warm-blooded animals that a study of the former can not but be of aid in understanding the laws governing vital activity.

The physiology of the frog, the classic laboratory animal, has been studied long and well, and much of our knowledge of the physiology of cold-blooded animals rests upon observations with this relatively small amphibian. But information with regard to the physiology of the frog is not so directly applicable to human physiology, for the frog in many respects differs widely from the warm-blooded human. It is a small animal.<sup>2</sup> It is distinctly aquatic, living for the larger part of the time in water, a medium for heat absorption and equalization of temperature altogether different from that surrounding warm-blooded animals in general and especially man. It is perhaps because of the frog's aquatic nature that one is most critical of the application of knowledge concerning the physiology of the frog to the interpretation of problems in human physiology. For comparative purposes, cold-blooded animals must be divided into three great classes, (1) those living in water, such as fish and turtles, (2) those living in air, such as most of the snakes, tortoises and lizards, and (3) those living

<sup>1</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 611.

<sup>2</sup> With the development of the ingenious and accurate micro-calorimeter of L. Algera (*Proc. Section of Sci., Royal Acad. Sci., Amsterdam*, 1931, **34**, p. 906) the potentiality of experimenting with very small cold-blooded animals is greatly enhanced.

both in air and water, such as the frog. It is clear from this classification that the animals living in air, such as the snakes, tortoises and lizards, exist more nearly under many of the life conditions of man.

Not only is it important to study cold-blooded animals living in air for the closest comparison with humans, but to make the study more strictly comparable, large animals are preferable. The structure of the body, the body weight, and the amount of surface area<sup>1</sup> exposed to the air should for such a comparative study be as nearly as possible the same as in the well-known studies of warm-blooded animals. Hence large cold-blooded animals are necessary. The frog for this purpose is of little value, for not only *different species* of frogs but *individual* frogs have in previous researches<sup>2</sup> shown a wide variability in heat production, a variability far greater than the normal, rather considerable variability found in individuals among the warm-blooded animals. Secondly, the activity of the frog is always uncertain and is perhaps greater than that of any other cold-blooded animal save the fish, and activity during any experimental period is detrimental to securing observations of value for comparative purposes. It is illogical to compare the metabolism of an active frog or fish with that of a man resting quietly or with that of a dog, a rat or a goose in complete muscular repose. Another advantage in using large cold-blooded animals for comparative physiology is that it is desirable to apply the same experimental methods employed for humans or warm-blooded animals to cold-blooded animals, and since the metabolism with the latter is so low, it is necessary in applying these methods either to study large animals or to conduct long experimental periods. Therefore the frog, by reason of its small weight, is ruled out. Furthermore, the frog is decidedly seasonal in its responses. Thus, the summer frog is different from the winter frog. These characteristics introduce several extraneous factors.<sup>3</sup>

In pursuance of its program of research in comparative physiology, the Nutrition Laboratory therefore decided to study *large* cold-blooded animals living in the air and not to include the fish (a most important economic problem) or any amphibious animals. To secure such animals became a matter of great concern. In the temperate zone there are only relatively small land tortoises, the turtles, even the large snapping turtle, being aquatic. There are no large snakes in the northeastern part of the United States, and it is only in the South that one can find relatively large rattlesnakes. The problem of obtaining suitable material, therefore, was an acute one. The technique of maintaining under normal laboratory conditions standard warm-blooded animals such as the dog, the rabbit and the guinea-pig, and a standard cold-blooded animal such as the frog has been well

<sup>1</sup>The surface area concept is, on historical grounds, retained throughout this book and finally completely disclaimed. A problem arose in writing this report in that zoologists may possibly find the results even more of interest than physiologists. Hence much that is obvious to the metabolism expert is necessarily included.

<sup>2</sup>Tigerstedt, R., Winterstein's Handb. d. vergl. Physiol., 1910-1914, 3 (Pt. 2), pp. 33 and 40. See, also, A. Krogh, Internat. Zeitschr. f. physik-chem. Biol., 1914, 1, p. 497.

<sup>3</sup>Rubner (Sitzungsber. d. preuss. Akad. d. Wissensch., 1924, 17, p. 230) has emphasized the importance of studying tropical animals. Fortunately nearly all our animals come under this head.

worked out, but large cold-blooded animals are as yet an unknown factor for the average laboratory technician. Hence our only recourse was to go to a large zoological park,<sup>1</sup> especially well equipped with a collection of reptiles, and we naturally turned to the New York Zoological Park, primarily because one of the foremost herpetologists in America, Dr. Raymond L. Ditmars, was in charge of the extraordinary collection there. We were fortunate in establishing most cordial relations with Dr. W. T. Hornaday, the director at that time of the New York Zoological Park, and always secured unfailing attention and advice from Dr. Ditmars. This deeply appreciated cooperation, coupled with the splendid collection of reptiles in the New York Zoological Park, resulted in our equipping in that Park a special laboratory for the study of the metabolism of large, cold-blooded animals. As can be seen from frequent reference to him in these pages, this report owes its existence in no small part to the ever-ready cooperation of Dr. Ditmars. All of his cooperation has been fully approved by the present director, Dr. W. Reid Blair.

<sup>1</sup>Two visits to the Carl Hagenbeck Tierpark in Stellingen-Hamburg, Germany, in the personal company of Dr. Ludwig Zukowsky, the Scientific Director of the Park, brought out many points that have been helpful in presenting the material in this report. We are much indebted to Dr. Zukowsky for his many courtesies and the most valuable information which he kindly gave us.

## PLAN OF RESEARCH

Our first experiment at the New York Zoological Park was made in October 1915, and the observations there continued until the summer of 1921 with, however, several long periods of interruption due to the exigencies of the World War. Supplementing these observations, special measurements were likewise made at the Nutrition Laboratory in the spring of 1920 and in the fall and winter of 1930-1931.

In the special problems of handling these unusual and at times dangerous animals, we relied upon the great skill of the late Mr. Charles E. Snyder and Mr. John Toomey of the New York Zoological Park. When the research first began in New York in 1915, Mr. Colbert Mason of the Nutrition Laboratory staff was in direct charge of the respiration experiments. After one year of intensive and successful experimenting, Mr. Mason resigned. The experimental work was then placed in the hands of Mr. E. L. Fox of the Nutrition Laboratory, whose skill and fidelity in these long and most tedious observations can hardly be overemphasized. A preliminary statement with regard to certain features of the research has already been made in conjunction with Mr. Fox and presented before the National Academy of Sciences.<sup>1</sup> Practically the entire experimental routine and the collection of nearly all the data presented in this book have been in Mr. Fox's hands, as will be evident by the constantly recurring text references to his aid in this study.

*Animals used*—The kinds of cold-blooded animal studied, the number of each kind, and the number of days on which experiments were made are as follows:

<i>Kind and Number of Animals</i>		<i>Days Experimenting</i>	
Boa constrictors.....	14	With lizards.....	55
Pythons .....	5	With tortoises.....	111
Rattlesnakes .....	13	With alligators.....	8
Gopher snakes.....	4	With snakes.....	725
Lizards .....	8		
Alligators .....	2	Total .....	899
Tortoises .....	11		
Total .....			
	57		

The names, species, habitats, and certain characteristics of these animals were as follows:

Bull Snake, *Pituophis sayi* (Schlegel), southwestern United States. (Used only in a preliminary orientation experiment.)

Cuban Boa, *Epicrates angulifer* (Bibr.), Cuba and Porto Rico. (Boa B, 12 kg.)

South American Boa Constrictor, *Constrictor constrictor* (Linn.), tropical South America. (Boas A and D to N, inclusive.)

Black-tailed or Indian Python, *Python molurus* (Linn.), dark phase, southern India, Malay Peninsula and Java. (Small Indian Python or "Pepper," 6 to 7 kg., and "1931 python.")

<sup>1</sup> Benedict, F. G., and E. L. Fox, Proc. Nat. Acad. Sci., 1931, **17**, p. 584.

Regal Python, *Python reticulatus* (Seba), Burma and Indo-China, Malay Peninsula and Archipelago. (32-kg. python.)

African Python, *Python sebæ*. (An incubating python, about 4.5 meters long, at the National Zoological Park in Washington, D. C. See pages 95 to 114.)

Texas Rattlesnake, *Crotalus atrox* (Bd. x Gird), Texas to California, abundant near Mexican boundary. (2 to 5 kg.)

Texas Gopher Snake, *Drymarchon corais couperi* (Holb), olive phase, Texas and northern Mexico. (2 to 3 kg.)

Lizard, *Iguana tuberculata* (Linn.), tropical America. (about 1 kg.)

American Alligator, *Alligator mississippiensis* (Daudin), southeastern portion of United States. (53 kg. and 4 kg., respectively.)

Radiated Tortoise, *Testudo radiata*, from Madagascar. (Used only in orientation experiment.)

Gopher Tortoise, *Gopherus polyphemus* (Daudin), southeastern United States. (Tortoises A to D, inclusive, 5 to 6 kg.)

South American Tortoise, *Testudo denticulata* (Linn.) (Tortoises Y and Z, 1930. 5 kg.)

Galapagos Tortoise, *Testudo nigrita* (Gray), found in the Galapagos Islands, a small group in the tropical Pacific, and Aldabra Islands in the Indian Ocean. (Tortoise E, 69 kg.)

Aldabra Tortoise, *Testudo elephantina* (Dum and Bibr), Aldabra Islands. (Tortoise F, 80 kg.)

Galapagos Tortoise, *Testudo vicina* (Gunther), Galapagos Islands. (Tortoise G, 132 kg.)

*Living conditions during captivity*—The extraordinary skill of Dr. Ditmars in the collection and care of the reptiles assured us of the closest approximation to normality possible in an animal in confinement. Liberal space, well-lighted, heated and ventilated, and food selected to promote well-being and longevity made the most acceptable substitutes for life in freedom. Lack of exercise has a pronounced effect upon the metabolism of warm-blooded animals, as is shown by the experiments of Lusk<sup>1</sup> on a dog confined to the laboratory throughout the winter and then allowed free run in the summer. Fortunately with snakes, lack of exercise plays a relatively small rôle, as they are normally inert and do not travel far or fast. On the contrary, tortoises and lizards are much more active, and confinement may influence their metabolism. The alligators that we studied lived in a large pool with ample space for exercise, and the lizards and tortoises likewise had considerable space for exercise. The temperature of the various animal cages was kept as nearly as possible that normal for the reptile. Ideally, it is better to study animals under conditions approximating as nearly as possible those prevailing in their usual habitat, with normal food, exercise, light, variations in climate and possibly seasonal variations in food. In the northern states snakes hibernate; in the South they do not. But in the New York Zoological Park no seasonal variation in temperature was permitted, and the animals were kept at essentially a normal summer temperature for them. Thus, for all the snakes, including boas, pythons,

<sup>1</sup> Lusk, G., Journ. Biol. Chem., 1915, 20, p. 565.

gopher snakes, and rattlesnakes, the temperature of the air in the dens was between 22° and 24° C., and the temperature of the gravel on which the snakes usually lay was 30° C.<sup>1</sup> The temperature of the water in the alligator pool was held at about 22° C. A long heating pipe running through the pool controlled the temperature of the water. The tortoises were kept in a chamber at essentially the same temperature as that of the snake dens. Of the various conditions of life in captivity, it is probably true that snakes are less influenced by the monotony of existence than are other animals. Particularly is it true that exercise in captivity is at a minimum, and food and exercise are the two factors affecting most profoundly the metabolism. So far as food is concerned, every effort was made to approximate the conditions of wild life. The whole problem of the care and feeding of reptiles has been most carefully studied by Dr. Ditmars.<sup>2</sup> Usually captive snakes take food of their own accord, but occasionally certain specimens were stuffed when they had refused food for a long time.<sup>3</sup> The life and the food of these reptiles in the Park were not wholly a normal outdoor life and food, but were approximately so. In any event, as has frequently been stressed by Dr. Hornaday, all the animals in the Park are saved the continual contact with dangerous enemies, a factor that would normally make for better living conditions and better health. Furthermore, the animals do receive good care if they are ill, and are artificially fed if they are not inclined to take food naturally. On the whole, therefore, the captive animal at the New York Zoological Park lives under conditions favorable for a normal existence.

*Measurements made*—With reptiles, particularly the large serpents, many of them not only difficult but dangerous to handle, the measurements were naturally somewhat limited. The chief measurements taken were of the rectal temperature, the skin temperature, and most important of all the gaseous metabolism, primarily the carbon-dioxide production, but in the 1930 and 1931 experiments also the oxygen consumption and the respiratory quotient. Direct calorimetry was attempted with one of the boas and with the 1931 python, but proved to be negative. (See page 423.) The heart rate of two of the tortoises was determined on several occasions. The surface area of several of the snakes was likewise obtained from girth and length measurements, and in the case of the 1931 python and one of the 1930 tortoises the skin area was actually measured. It was possible to determine the weight of the skeleton of one snake and with the tortoises to make allowances for the amount of inactive shell. The relative activity during the gaseous metabolism measurements was recorded, although not quantitatively, and a few observations upon the respiration rate, the excretion of water vapor and the insensible perspiration were secured. In a few instances analyses of feces and urine were made. Our chief study, however, centered around the calculation of the heat production from the measured carbon-dioxide production or oxygen consumption.

<sup>1</sup>Krehl and Soetbeer (Arch. f. d. ges. Physiol., 1899, 77, p. 634) state that at the Hamburg Zoological Gardens the snakes' cages are heated to 30° C.

<sup>2</sup>Ditmars, R. L., Zoologica, 1912, 1, p. 197.

<sup>3</sup>F. W. FitzSimons (*Pythons and their Ways*, London, 1930, p. 20) also discusses the method of forced feeding of serpents and feeding in captivity.



*Conditions of measurement*—In any comparison of warm-blooded with cold-blooded animals it is essential that both types of animals should be studied under the same conditions so far as absence of activity and of food is concerned. Perhaps no one problem is more confusing in making studies in comparative physiology than the differences in activity of the various animals used. It is impossible to compare animals other than upon the basis of complete muscular repose. A quiet, well-trained dog or rat or a man in complete repose can not be compared with another animal engaged in any amount of muscular activity. The amount of activity possible during confinement in a cage is, to be sure, somewhat limited but nevertheless this factor presents one of the greatest difficulties in making the comparisons. In this respect the snakes were ideal subjects. Ordinarily they remained hours at a time without movement, differing greatly from frogs which are usually very active and can not be relied upon to remain quiet. Indeed, our observations on snakes were for the greater part secured during complete muscular repose, a factor always stressed in the measurement of the basal metabolism of humans. The tortoises were, on the other hand, more active than the snakes and hence our observations on them frequently do not have the comparative value of those made with the large snakes. The influence of food and digestive activity in stimulating metabolism is well known. As a result, every effort is made with warm-blooded animals to study them in the post-absorptive condition. Fortunately reptiles, and snakes particularly, can live for long periods without food, so that it is possible to rule out the period of active digestion and study these animals in the post-absorptive condition. The effect of the digestive process may likewise be studied, as many of our protocols show.

*Special objects of research*—One of the special objects of our research was to study the gaseous metabolism of *large* cold-blooded animals, since it is much more logical to compare the metabolism of a human with that of a large cold-blooded animal than it is with that, for example, of a small frog. It would be necessary to multiply the metabolism of one small frog several thousand times to bring the frog up to the corresponding weight of a man. On the other hand, if one thousand frogs were studied simultaneously in an attempt to secure a weight of frogs equivalent to the weight of a man, 973 of these frogs might be active during the period of measurement and 27 quiet, or *vice versa*. In other words, the individuality of the frog not only as regards its own individual metabolism, which has been found to vary enormously, but particularly as regards its tendency to activity confuses the issue greatly. The small weight and the small area of the frog, therefore, make it difficult to compare it at all with man or even with the larger cold-blooded animals such as the alligator, the large snakes and the tortoise. For comparison with a man weighing on the average 60 kg. it was desirable, if possible, to secure a cold-blooded animal weighing approximately this same amount. As a matter of fact, although much of our work was carried out with snakes weighing only from 5 to 15 kg., we had one python weighing 32 kg., an alligator weighing 53 kg.,

and a Galapagos tortoise weighing 132 kg., approximating the mass of a fat man. Hence the metabolism of these particular animals per unit of weight or per unit of area could be, at least roughly, compared with the metabolism of man without making too great assumptions in the matter of activity, because only one animal was under study at one time and not several and the activity or absence of activity could be definitely recorded. Large snakes also are of advantage in studies of comparative physiology because they can be studied without food over a long period of time. Indeed, snakes have been known to live without food for two years. In such cases the animal may finally weigh only half its original weight (see the fasting data for our boa D, for example, pages 163 to 168), and thus the influence of size may also be studied, although, to be sure, the factor of fasting or undernutrition enters into the comparison here.

### PROBLEMS STUDIED

*Environmental temperature*—In planning our research, we selected for study those problems that, by applying the special Nutrition Laboratory techniques, we considered would probably be the most productive of results. The well-known fact that with cold-blooded animals the metabolism decreases as the external temperature is lowered demanded immediate study. It was impossible to consider with the cold-blooded animals a *basal* metabolism. The very definition of *basal* metabolism as applied to warm-blooded animals means the minimum metabolism compatible with normal life and under conditions involving complete muscular repose and the absence of digestive activity. With the cold-blooded animals in general the metabolism decreases as the temperature goes down, the animal becomes dormant, and gradually passes into a state approximating “suspended animation.” The most notable instance of this phenomenon is the much discussed and debated freezing of fish, first brought to public attention by Raoul Pictet.<sup>1</sup> It is therefore immediately conceded that no definition of basal metabolism as applied to warm-blooded animals can be thought of here. The metabolism reaction at different temperatures has been carefully studied with the frog and some small reptiles, and it was imperative that this be one of the first problems studied with our large cold-blooded animals. The well-known change in the velocity of chemical reactions with increasing temperature, the so-called “Van’t Hoff law” or the “ $Q_{10}$  law” (according to which the velocity of the reactions increases two or three times for each change of 10° C. in temperature) was therefore our first problem to be studied.

*Size*—The second problem was the metabolism of various cold-blooded animals of the *same species* as affected by size. With most laboratory animals, a study of the influence of size can be admirably combined with

<sup>1</sup> Pictet, R., *Revue Sci.*, 1893 (cited by J. Lefèvre, *Chaleur Animale et Bioénergétique*, Paris, 1911, p. 241). Pictet’s experiments are also cited by W. Marcet (*A Contribution to the History of the Respiration of Man*, Croonian Lecture, London, 1897, p. 13), who mentions observations of his own that are not fully in accord with Pictet’s findings. Pembrey (Schaefer’s *Text-Book of Physiology*, London, 1898, 1, p. 817) likewise reports the experiments of Pictet.

a study of growth, as one can measure the metabolism of an animal when young and then measure it again when older. In a zoological park it is practically impossible to determine the metabolism of a young snake and then wait until it grows to an adult, particularly in the case of large serpents. The growth is relatively small, very slow, and the mortality, even under ideal conditions, is high. One would therefore run the risk of studying a youthful organism and before it had reached a much larger size death might have occurred, so that one could not study the effect of growth. It was possible, however, to compare small and large pythons and small and large boas, and this was done.

*Deposition of fatty tissue*—Another problem considered was the effect upon metabolism of the deposition of fatty tissue. A fat snake could be compared with a thin snake, and it was possible to do this with the same snake, although this involved a study of prolonged inanition.

*Fasting and prolonged undernutrition*—The incredible length of time that cold-blooded animals can live without taking food makes the study of undernutrition or prolonged fasting especially advantageous. Hence observations on the course of the total heat production from day to day and the course of the heat production per unit of weight and per unit of surface area in long-continued fasting experiments were of special interest in our experimental program. When we consider that a cold-blooded animal as large as a giant python may subsist on its own tissues for nearly two years, not in moribund hibernation but at a temperature of approximately 26° to 30° C., which ordinarily prevails in the reptile house of a zoological park, and when we consider that during this time the draft upon body material is not such as to make the animal so emaciated as to be unsuitable for exhibition purposes, we see immediately the possibilities for studying the influence upon metabolism of prolonged drafts upon body material.

*Digestion*—With warm-blooded animals the influence of digestion, which is usually rapid and extensive, can be readily studied. With some of the birds the period of digestion may be distinctly short—a few hours. Usually with humans it is considered that the period of active digestion ceases after 12 hours, when the post-absorptive condition is reached. With ruminants this period is protracted to from 24 to 36 hours, or even longer. The length of the digestive period with the large cold-blooded animals has not been known. In wild life their feeding is uncertain and they experience long periods without food. Hence in beginning an experiment with a snake, the results of which are to be used for comparison with those obtained on other snakes or on warm-blooded animals, one should be fairly certain that the metabolism approximates the *post-absorptive* condition. Owing to its uncertain eating habits, especially in confinement, the cold-blooded animal may be in a low state of nutrition. It is especially desirable, therefore, to study with those particular animals that are capable of prolonged fasting and characterized by a low metabolism, the stimulus to metabolism derived from the taking of food. The effect of the various kinds of food should first be noted. Usually animals in the wild, especially snakes, eat animal food with a relatively large amount of protein. But it is possible by artificial feeding to give a large amount of fat, as was done with several of our snakes.

The influence of the environmental temperature upon the course of the heat production during digestion should also be studied, that is, the metabolism during digestion at 20° C. should be compared with the metabolism during digestion at a much higher temperature, such as 30° C. or possibly 37° C., which would approximate the body temperature of warm-blooded animals. Three elements enter into this study of the influence of digestion at different environmental temperatures. First, there is the time element. How long does the period of digestive activity last? Second, what is the maximum heat production or the peak in metabolism and when does it occur? Third, what is the total increase in heat production above that in the non-digestive state caused by the ingestion of a definite amount of food? The difficulty with most of the serpents is the uncertainty as to the exact nature of the food, for one can not easily analyze beforehand a litter mate control representative of the rabbit, the guinea-pig, or the pigeon eaten by the snake. But approximate computations of the composition of the food eaten may be permitted. It is thus seen that in the field of digestion alone there are many important problems suggested for study with these large, cold-blooded animals.

*Respiratory quotient*—Although with most of the cold-blooded animals, protein and fat are the chief food materials and hence striking changes in the respiratory quotient would not be expected in the absence of carbohydrates, a study of the respiratory quotient with these animals was planned and as finally carried out, especially in the 1930 and 1931 series, led to some remarkable findings. Not only the character of the food but, even more striking, the environmental temperature produced profound alterations in the respiratory quotient. Time was not available, however, for an extended study of the significant relations between temperature of the environment and the respiratory quotient.

*Muscular work*—The influence of muscular activity upon the metabolism of cold-blooded animals has been studied practically only with the excised gastrocnemius muscle of frogs. It would therefore be important to study, if possible, the effect of muscular activity upon the intact animal. It is, however, practically out of the question to compare the efficiency as a machine of a cold-blooded animal with that of a warm-blooded animal, for one can not measure the work done by cold-blooded animals. In some of our observations it was noted that after the animals were handled and transferred, for example, from one cage to another, there was frequently a high production of carbon dioxide. The questions therefore arise: Is this high metabolism possibly caused by the exposure to a higher temperature in a new environment, is it the result of struggle, that is, is there an increase in heat production as with muscular work, or is it possibly due to a psychic agitation or tension caused by the insult to the animal received in handling? The cause may be classified under the head of muscular work, psychical state, or agitation. A number of experiments were made to contribute to this point.

*Comparison of snakes with other cold-blooded animals*—As a result of observations on these animals in the post-absorptive condition, it was pos-

sible for us to compare directly the metabolism of the snake with that of the tortoise, the lizard and the alligator, referred to body weight and to surface area, or more properly to the two-thirds power of the body weight. This comparison enables a study of the comparative physiology of cold-blooded animals of greatly varying sizes and supplements the literature on small animals in such a way as to extend the metabolism measurements on cold-blooded animals of widely different species into the range of large body weights.

*Comparison of metabolism of cold-blooded animals when raised to a temperature approximately that of homoiotherms*—In certain instances, particularly with the snakes, it was possible to raise the temperature of the environment to such a height that the animals themselves had a body temperature not far from that of homoiotherms, that is, approximately 37° C., and a comparison of the metabolism of the cell tissues when the cold-blooded animals were at this temperature with that of warm-blooded animals became one of our most important problems.

*Mechanism of heat loss in snakes*—Because of the profound influence of environmental temperature upon the metabolism of the cold-blooded animal and because of the general tendency of the animal to assume the temperature of the environment, the mechanism of heat loss in the snake acquires special importance. One of our first problems, therefore, was the study of the skin temperature of the various snakes compared with their rectal temperature and the temperature of the environment. A large number of measurements were made for this particular study, which give information upon the rapidity with which the snake assumes the environmental temperature, and the difference between the skin, the rectal and the environmental temperature. With the use of a calorimeter at the Nutrition Laboratory in Boston direct calorimetry was attempted, to measure any direct radiation of heat. Such measurements have been successfully accomplished with animals living in water, by Rubner<sup>1</sup> with his micro-calorimeter and later by A. V. Hill,<sup>2</sup> but with animals living in air the problem had to be studied by entirely different methods, with a ventilated chamber. The direct calorimetry proved to be an entirely negative study, and immediately the heat of vaporization of water assumed great importance. This was studied in connection with the ventilation rate and the humidity of the air of the respiration chamber in which the snake was placed.

*Particular features of observations on tortoises in 1930*—Snakes were used in the study of most of these problems. A number of lizards, which likewise live in the air, were also available, and the observations made upon them included practically the same problems as were investigated with the snakes. Two alligators were studied in the earlier stage of our experimental program, but only when not submerged in water. The problems outlined above were not, however, studied in detail with these alligators. Next to the snake in the number of observations made upon it was the tortoise. The

<sup>1</sup> Rubner, M., *Tigerstedt's Handb. d. physiol. Methodik*, 1911, **1**, Abt. 2, p. 218.

<sup>2</sup> Hill, A. V., *Journ. Physiol.*, 1911-1912, **43**, p. 261.

animals available ranged in size from the 5-kg. gopher tortoises to a giant Galapagos tortoise of 132 kg. With the tortoises studied between 1915 and 1917 more difficulty was experienced in securing quiet periods than with the snakes. Hence there were fewer consecutive experiments, and many periods had to be rejected. For this reason further observations were made upon two 5-kg. tortoises in 1930. In this later series the main problems studied duplicated for the most part those with the snakes. Thus, attention was given to the influence of environmental temperature and the influence of digestion upon the respiratory metabolism, and in addition efforts were made to secure accurate determinations of the respiratory quotient. The calculation of the metabolism per unit of weight and per unit of surface area presented special difficulties in the case of the tortoise, because of the large proportion of inert matter (shell) making up its body weight. Hence one of the 1930 tortoises was killed, and the weight of shell and the flesh weight were actually determined. Finally, certain abnormal characteristics of the mechanics of respiration were studied. Muscular and digestive activity were ruled out only with difficulty in the case of the tortoise, but a sufficient number of observations were obtained in the two series with this animal to permit of making reasonable comparisons.

*Particular features of observations on the 1931 python*—Although an extensive series of respiration experiments and other observations were made upon snakes from 1915 to 1921, it seemed important in 1931 to confirm and amplify certain phases of this earlier investigation by measurements upon a python with more modern technique. One of the main objectives of the 1931 research was to make a more complete comparison of the rectal and environmental temperature, since it was clear that the relationship between the temperature of the body and that of the environment of the snake has an important bearing upon the heat lost by vaporization of water. The earlier temperature studies were not satisfactory because, although the environmental temperature might have been closely recorded, the rectal temperature measurements were at best only imperfectly obtained. Furthermore no observations had been secured during digestion, and one of the special features of the 1931 series was to determine what is the effect of digestion upon the body temperature. In the earlier snake series the respiratory quotients were as a whole considered unsatisfactory, owing to the technique (see page 150), and the second objective of the 1931 research was to determine the respiratory quotient accurately by more perfected technique. A third objective was the measurement of the insensible perspiration and the water output. Only a few observations regarding these two factors had been made prior to 1931, but it was believed that the relationship between the water vaporized and the heat lost by the snake is such that quantitative measurements of the water vapor and the insensible perspiration were imperative. Moreover, although the metabolism of a few snakes, notably the rattlesnake, had been measured at 37° C., it was felt desirable to secure more observations at this high temperature with another and a larger snake. The measurement of the surface area of the snake and particularly the determination of the constant to be



employed in calculating the surface area were seriously questioned when we analyzed our earlier data. To supplement the measurements of girths and lengths obtained upon snakes in the earlier series, the same measurements were made upon the 1931 python and, in addition, at the end of the entire experimental program the python was killed and the skin was removed, photographed and measured. The fragmentary observations on direct calorimetry obtained with a boa in 1920 were substantiated by a second series of direct heat measurements on this python, with a view to determining to what extent water vapor is a path for the loss of heat in the snake, whether sensible heat as such is given off by the snake, and, if so, under what conditions. The fact that a considerable increase in the respiratory metabolism of the cold-blooded animal can take place during digestion was repeatedly demonstrated. The 1931 program included measurements of skin temperature, rectal temperature, respiratory metabolism, water vapor and insensible perspiration *during* digestion. In addition, further data were secured on the gaseous metabolism at different environmental temperatures, and incidental observations were obtained with regard to feces and urine.

*Body temperature during incubation*—In the spring of 1931, when the manuscript of this report was nearly completed, opportunity was had to make a careful survey of the environmental and the body temperatures of an incubating python, while coiled over her eggs. This study was made at the National Zoological Park at Washington, D. C., thanks to the co-operation of the Director, Dr. William M. Mann, and his assistant, Mr. F. O. Lowe, to both of whom we are deeply indebted.

It is thus seen that our research dealt in large part with the measurement of the total metabolism of large, cold-blooded animals, with special reference to their relative size, their environmental temperature, and the digestive activity, employing for this purpose cold-blooded animals of such varying form, nature and chemical composition as the python, on the one hand, and the Galapagos tortoise with its large preponderance of inert bony structure, the shell, on the other. As our investigation progressed, it became clear that a large number of problems had been by no means adequately studied, and many other problems suggested themselves concerning not only the development of the experimental side of the technique and the experiments themselves, but particularly concerning the mechanism of heat production and heat loss. We shall therefore frequently allude to unsolved problems that await immediate attack. Unfortunately this attack can not be expected from the Nutrition Laboratory.

## TECHNIQUES EMPLOYED

### METHOD OF STUDYING THE GASEOUS METABOLISM

Since these observations dealt for the most part with the respiration rate, the body temperature, and especially the gaseous metabolism, the technique in the New York series of measurements was confined almost entirely to body-temperature measurements and the measurement of the carbon-dioxide production, with occasional determinations of the oxygen consumption. As the investigation progressed and it began to be evident that there was a relationship between the water vapor and the heat production of these cold-blooded animals, determinations of the water vapor assumed unusual importance and in many experiments the water vapor was therefore directly measured. To determine the gaseous metabolism, a special metabolism laboratory was equipped at the New York Zoological Park with a number of respiration chambers that had been designed, constructed and tested at the Nutrition Laboratory in Boston especially for this purpose. Later, in the 1930 series of measurements on two South American gopher tortoises and in the 1931 observations on a python carried out at the Nutrition Laboratory, respiration apparatus were employed that were similar in many respects to those used in New York but which embodied some accessory features of technique and which enabled accurate measurements of the oxygen consumption as well as the carbon-dioxide production, thereby permitting a determination of the respiratory quotient.

Many of the earlier researches dealing with cold-blooded animals have been carried out on fish,<sup>1</sup> an aquatic animal demanding a type of respiration apparatus different from that required for air-living animals. With animals living in air and producing small amounts of carbon dioxide per minute, such as the frog, some micro type of apparatus has ordinarily been employed. Since this present research deals with large animals living in air and since one of the reasons for selecting these animals was that a technique might be used comparable to that employed for humans, all observations with these large cold-blooded animals were made with relatively large respiration apparatus calling for the regularly established Nutrition Laboratory technique that has been in use for years in metabolism observations on children and adult humans.

*General principle of respiration apparatus*—In general principle these respiration apparatus consisted of well-ventilated chambers of the closed or open circuit type in which the carbon dioxide produced by the animal was removed from the air current by a suitable absorbent and pure oxygen was added to the system as needed to replace that consumed by the animal. Each chamber was provided with a small expansion chamber or spirometer.

<sup>1</sup> Rubner, (Biochem. Zeitschr., 1924, **148**, p. 223) has strikingly pointed out the difficulties of using fish in such studies.

## RESPIRATION APPARATUS USED IN NEW YORK EXPERIMENTS

Respiration chambers of various sizes were employed, in that the chamber was practically fitted to the animal. This was literally the case with the largest tortoise, the animal being measured carefully beforehand and the chamber constructed to fit exactly its size. In the beginning two respiration chambers were used with a capacity of 85 and 75 liters, respectively,

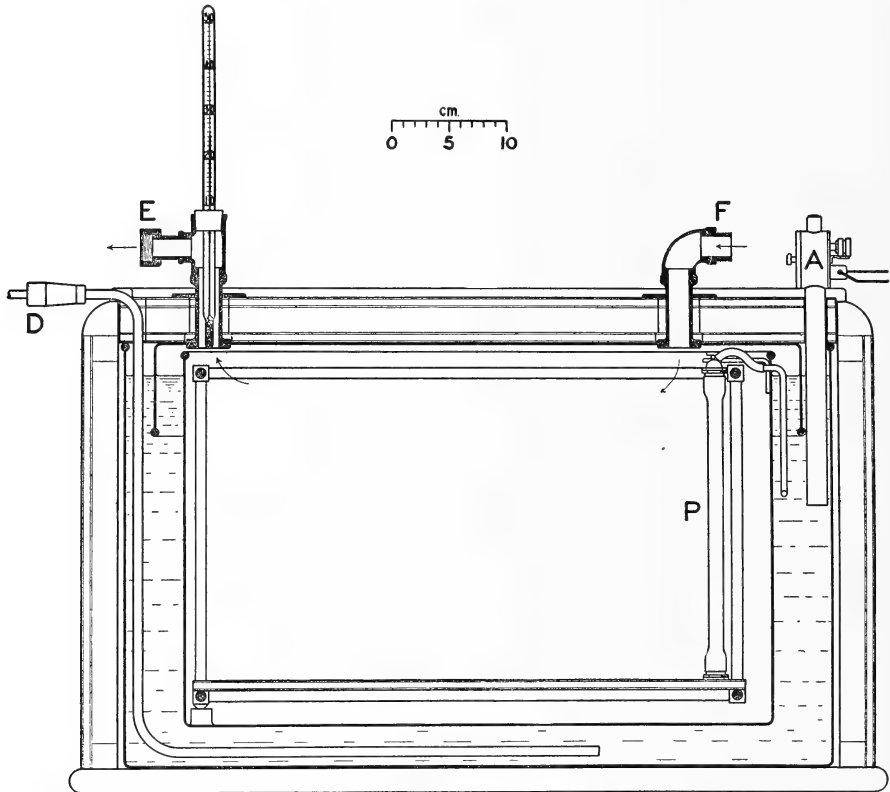


FIG. 1—RESPIRATION CHAMBER (85-LITER VOLUME) FOR LARGE COLD-BLOODED ANIMALS.

A, thermostat; D, electric heater for control of temperature of water bath; E, outlet pipe; F, intake pipe; P, pneumograph.

but these were soon found to be much larger than necessary and a subsidiary chamber, reducing the volume to about 27 liters, was used in the majority of the experiments. This supplementary chamber could be employed inside the 85-liter or 75-liter chamber and still retain provision for an air-tight water seal and a graphic registration of any activity that might occur. For the largest tortoise a chamber was constructed containing 908 liters. In this chamber various experiments were made with one large tortoise, two fairly large tortoises studied simultaneously, and a large alligator. For observations on a 5-meter python, which was too large

(from the standpoint of manipulation of the animal) to place in the 85- or 75-liter chambers and yet for which the 908-liter chamber was too large, a special recessed cover was constructed to drop inside the 908-liter chamber and thus reduce the volume to 339 liters.

The essential features of these chambers have already been briefly described.<sup>1</sup> The 85- and 75-liter chambers are of metal, double-walled, water-jacketed vessels protected with a covering of cork and canvas for insulation purposes. The metal cover, also protected by cork and canvas, dips into a water seal between the two metal walls, thus making the interior of the chamber absolutely air-tight (fig. 1). The cork and canvas casing is especially helpful in securing uniformity in the temperature of the respiration chamber, a point especially important in studying cold-blooded animals.

Air passes through the pipe, F, and enters the chamber near the top, at the right-hand side. The outgoing air leaves directly through the pipe, E, so there is a tendency for a maximum ventilation. A small baffle plate, not shown in figure 1, deflects the ingoing air downward. Figure 1 shows the electric heating device, D, and likewise the thermostat, A, for temperature control. The snake or other animal to be studied is placed in a metal cage, open at the top save for a wire-mesh cover to prevent the animal from escaping. This cage in turn is placed on a movable platform or floor inside the chamber. The record of the activity of the animal is secured in the usual way by suspending the floor at the left-hand end on pin points and supporting the right-hand end by a spiral spring (not shown in figure 1) and a small pneumograph, P. Any movement of the animal causes a change in tension on this spring, and the change in tension is transmitted by means of the pneumograph to a tambour and kymograph outside the chamber. Thus any activity of the animal is graphically recorded.

The 85- and the 75-liter chambers were soon found to be too large, and hence a supplementary chamber was designed to be placed inside the larger chamber (fig. 2). This inner chamber is suspended on a movable platform, as before, only we are now looking at it from the rear. The cover, K, of this inner chamber fits into a water seal, a, around the upper edge of the chamber. The original cover of the larger chamber that also dipped into a water seal has been removed and replaced by a wooden cover supporting two pipes, E and F, which terminate in enlarged cylindrical thin-walled tubes, each of which dips into a small water seal,  $b_1$  and  $b_2$ , on top of the cover, K, of the inner chamber, H. These water seals, which make air-tight closures for the pipes E and F, give perfect flexibility, so that any movement of the inner chamber up and down, due to the activity of the animal, is not hindered. Two screws,  $G_1$  and  $G_2$ , fit into the upright standards and allow one to raise and lower the pipes, E and F, when removing the cover or adjusting the apparatus. The small inner chamber, H, has a volume of 27 liters. The air enters the chamber through the pipe, F, and is deflected downward against the sides of the chamber by a baffle

<sup>1</sup>Benedict, F. G., Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1924, Abt. IV, Teil 10, pp. 530 *et seq.*

plate. It leaves through the tube, E. The temperature of the water bath in the outer chamber is controlled by the electric heater, D, and the thermostat, A. The majority of the observations were carried out with this subsidiary 27-liter chamber inside the larger chamber. A wire-mesh cover, B, was fastened just inside the cover, K, so that the chamber could be opened at the end of an experiment and the snake left inside overnight, if desired, without danger of its escape.

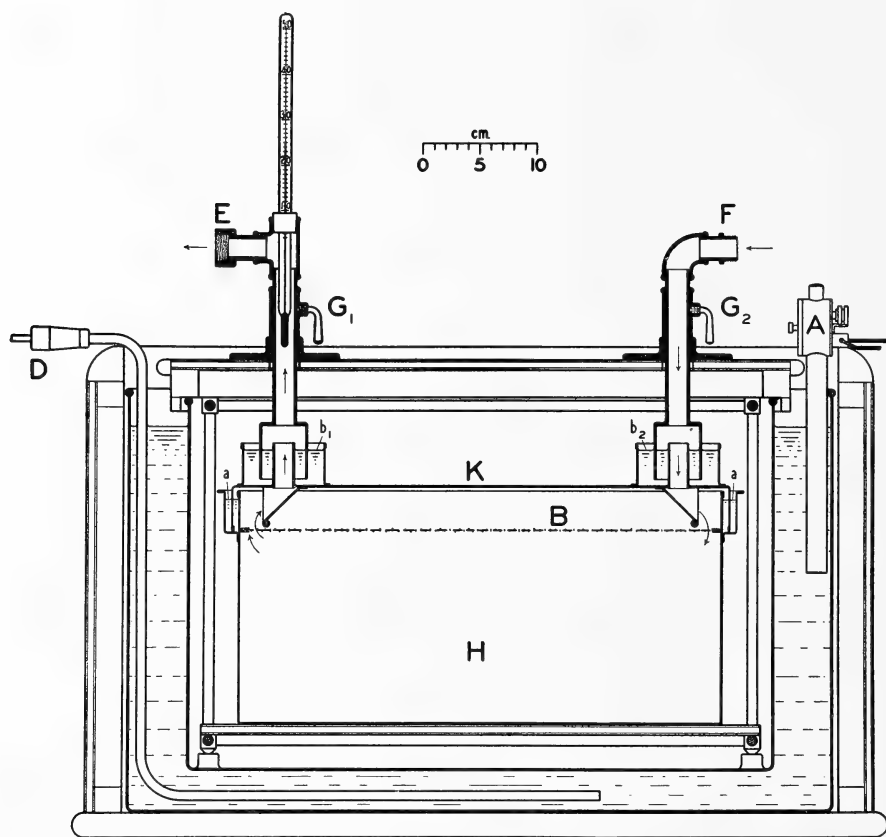


FIG. 2—RESPIRATION CHAMBER OF 85-LITER CAPACITY WITH SUBSIDIARY 27-LITER CHAMBER INSIDE.

H, subsidiary 27-liter chamber, with cover, K, in water seal, a; E, outlet pipe, and F, intake pipe dipping into water seals, b<sub>1</sub> and b<sub>2</sub>, respectively. G<sub>1</sub> and G<sub>2</sub>, screws to adjust height of tubes E and F; D, electric heater; A, thermostat; B, wire-mesh cover to prevent escape of snake when chamber is left open overnight.

Since our largest Galapagos tortoise weighed 132 kg., a respiration chamber was built to fit this animal. The tortoise was accordingly measured and a chamber 91.2 cm. wide, 81.4 cm. deep, and 122.3 cm. long, with a volume of 908 liters, was constructed of heavy galvanized iron. The outside was reinforced by boards. Around the top, on the outside, was soldered

a flange containing water for a water seal. Into this seal a metallic cover, A, with a rim about it could be lowered, to make a tight closure. (See the view to the left in figure 3.) Tubes in the side and top provided for the entrance and withdrawal of a ventilating current of air. To record the degree of repose or activity of the tortoises the usual Nutrition Laboratory method was employed, that is, one end of the chamber base rested on a crude approximation to a knife-edge, K. The other end was suspended on several leaves from a light wagon spring, S. A rubber ball, R, was placed beneath these leaves, so that any change in the center of gravity of the animal would alter the degree of pressure on this rubber ball, and the

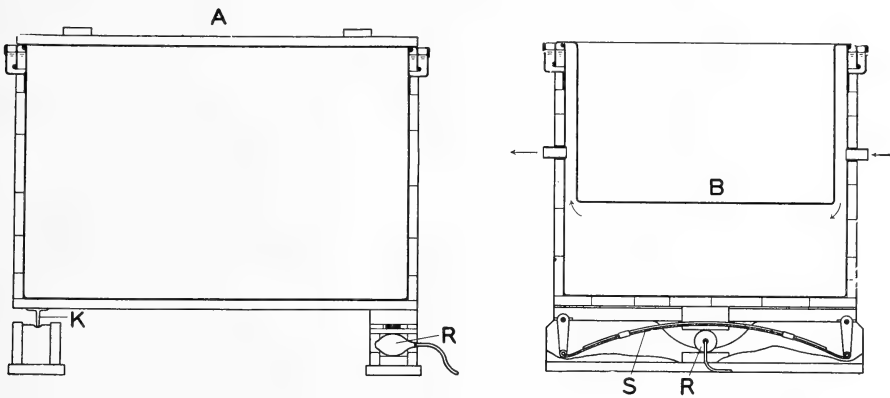


FIG. 3—RESPIRATION CHAMBER OF 908-LITER CAPACITY WITH RECESSED COVER FOR REDUCTION OF VOLUME.

One end of chamber rests on a knife-edge, K; other end is suspended on leaves from a buggy spring, S, beneath which is a rubber ball, R, connecting with a tambour and kymograph. Cover, A, is used when full volume of 908 liters is desired, the recessed cover, B, when a much smaller volume is preferable.

change in compression of the air in the ball was recorded by the usual tambour and kymograph. Thus the entire activity-recording equipment was outside the respiration chamber. It gave most satisfactory records and likewise showed that in many instances the tortoises were restless and undesirable animals for metabolism work; hence numerous periods had to be rejected on account of activity. Photographs of this 908-liter chamber are shown in figures 4 and 5.<sup>1</sup>

One or two of the animals, particularly the 5-meter python and the 53-kg. alligator, were too large for the 27-liter chamber and, on the other hand, were much too small to put into this 908-liter chamber. To reduce the volume of this large chamber, therefore, a special recessed cover, B (shown in place in view at the right in figure 3), was constructed. This recessed cover was provided with a lip or rim which could be dropped into the water seal attached to the large tortoise chamber. The cover was so

<sup>1</sup>The photographs shown in figures 5 and 6 were taken by Mr. E. R. Sanborn, the photographer of the New York Zoological Park.



constructed that it dipped down into the inside of the chamber close to the walls and, when in place, reduced the volume of air in the chamber from 908 to 339 liters. Both the large python and the alligator still had plenty of room to rest quietly beneath this recessed cover, and yet the chamber volume was perceptibly reduced.

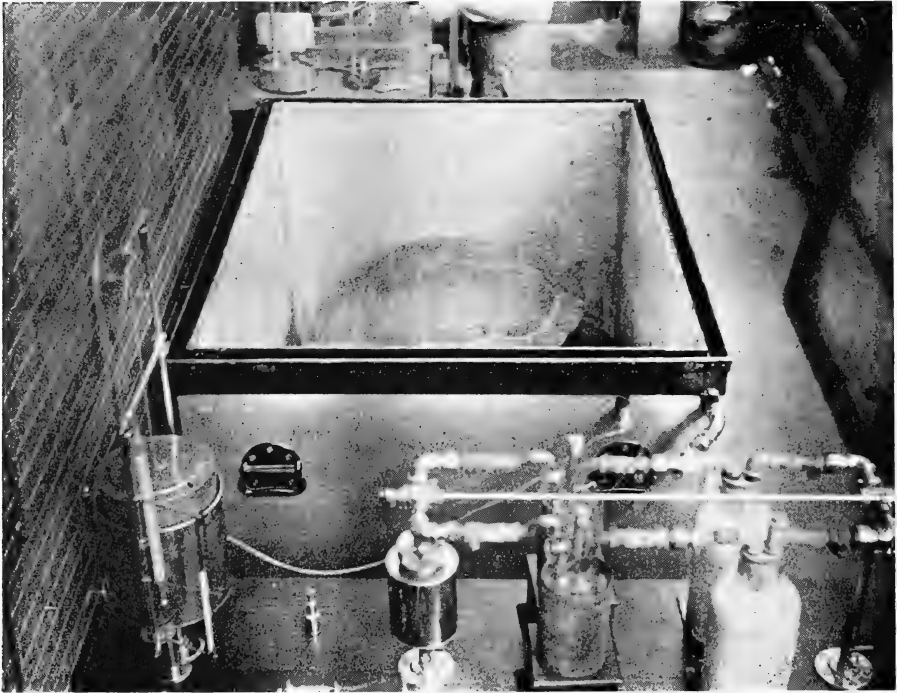


FIG. 4—VIEW OF A 62-KG. TORTOISE INSIDE 908-LITER RESPIRATION CHAMBER.

*Ventilation of the chamber*—These chambers were ventilated by the so-called “universal respiration apparatus,” which has already been described.<sup>1</sup> The usual Crowell blower of the positive type drew the air out of the chamber, forced it through sulphuric acid to remove the water vapor, and then passed it through a suitable absorbent for carbon dioxide. This absorbent was the ordinary Nutrition Laboratory soda-lime, in a special bottle. The air leaving this bottle was again passed through sulphuric acid to absorb any water vapor yielded to the air current in its passage through the soda-lime, and the change in weight of the soda-lime bottle and its following sulphuric acid bottle (weighed on a balance accurate to 0.01 gram) was recorded as the carbon dioxide absorbed. The volume of the universal respiration apparatus and the spirometer was about eleven liters. In figure 6 is shown the respiration chamber installed in

<sup>1</sup> Benedict, F. G., Amer. Journ. Physiol., 1909, **24**, p. 345; *ibid.*, Deutsch. Arch. f. klin. Med., 1912, **107**, p. 156; *ibid.*, Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1924, Abt. IV, Teil 10, p. 440.

the reptile house at the New York Zoological Park, with the universal respiration apparatus in the foreground. The ventilation rate could be adjusted by slowing the motor, or more particularly by opening a by-pass from one side of the blower to the other. By either of these means or by both the ventilation could be held at any desired rate, usually not far

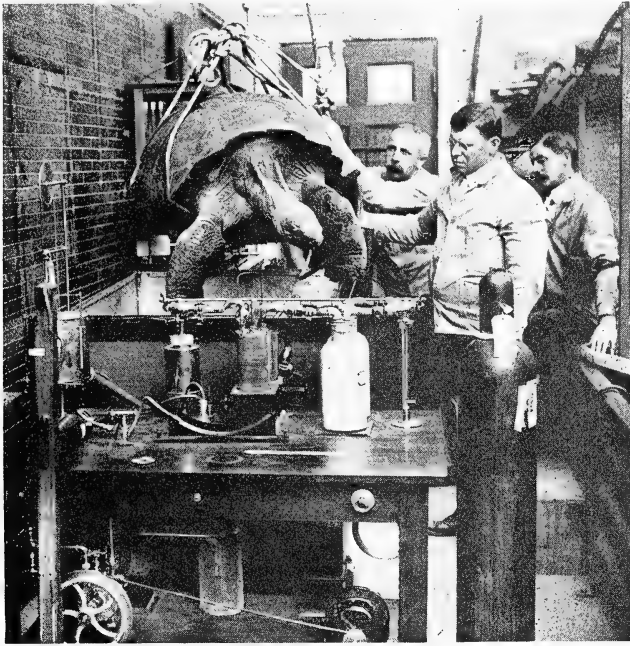


FIG. 5—LOWERING A 132-KG. TORTOISE INTO 908-LITER RESPIRATION CHAMBER.

from 3 to 8 liters per minute. Because of the small amount of carbon dioxide produced by these cold-blooded animals, especially at relatively low temperatures, the method was soon introduced of having only intermittent ventilation. Under these conditions the carbon dioxide was allowed to accumulate inside the closed chamber and at approximately definite periods (about once every 1 to 6 hours) the chamber was ventilated for about 15 minutes, the accumulated carbon dioxide then being removed and the air refreshed with oxygen. This ventilation was usually carried out at a high rate of speed, about 30 liters per minute. Undoubtedly this procedure did remove all the carbon dioxide, but it is equally certain that varying amounts of condensed water remained in the chamber from time to time, and hence water determinations as such were not made under these conditions. This intermittent ventilation made it possible to employ simultaneously two different respiration chambers ventilated by the same respiration apparatus (fig. 7), it being only necessary to provide a supplementary spirometer for the second chamber and two sets of sulphuric acid and soda-lime bottles

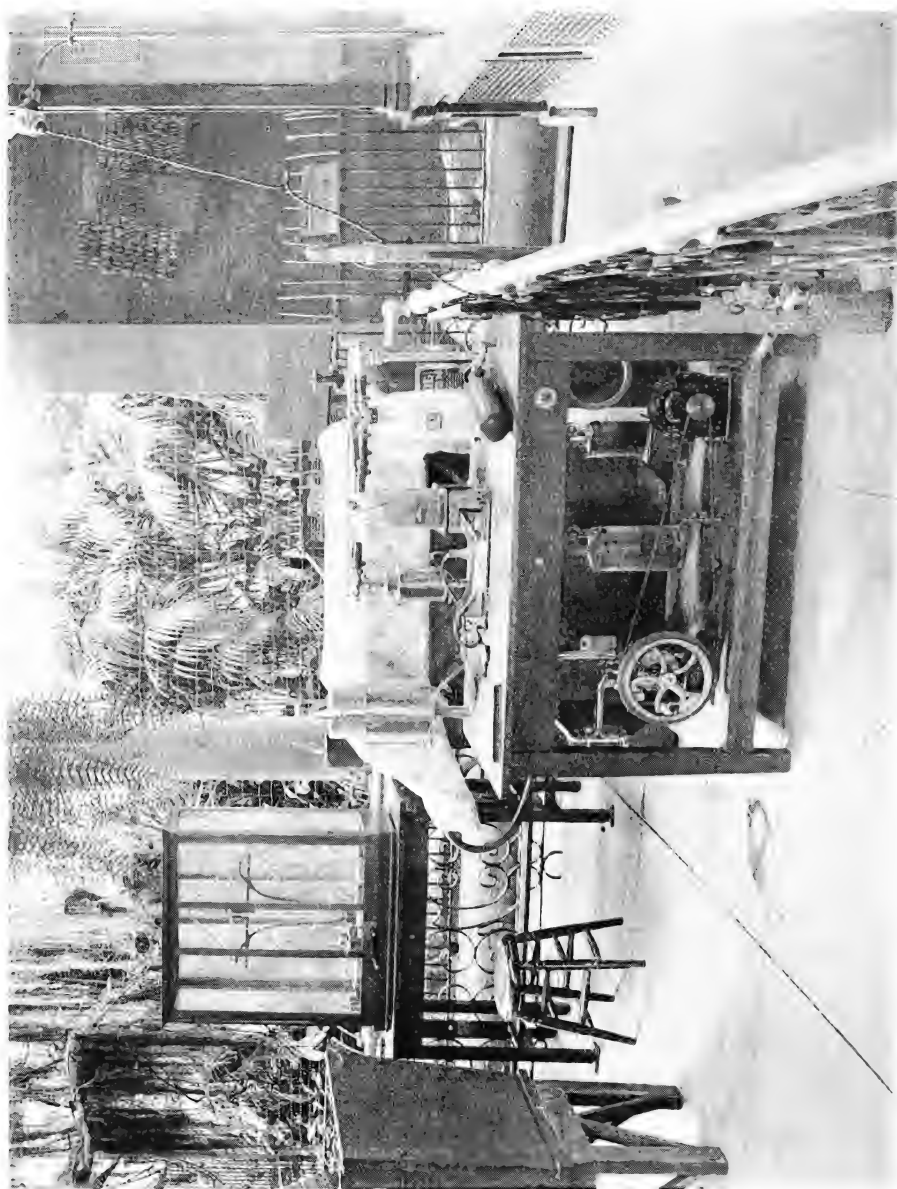


FIG. 6.—RESPIRATION CHAMBER (85-LITER) INSTALLED IN REPTILE HOUSE AT NEW YORK ZOOLOGICAL PARK.

for the universal respiration apparatus. Thus an animal could be allowed to remain in one chamber without ventilation until the carbon-dioxide content of the air inside had increased to 1 per cent of the total volume, an amount of carbon dioxide known to be in no sense injurious to animal life. The air in this chamber could then be swept out by rapid ventilation through one of the two sets of absorbing bottles. Meanwhile another ani-

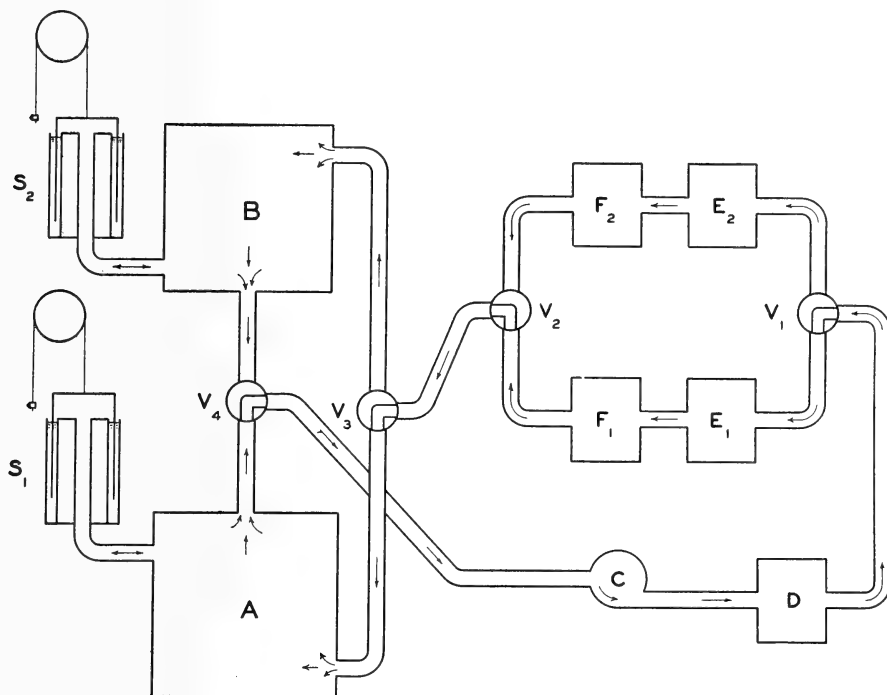


FIG. 7—SCHEMATIC DRAWING SHOWING SIMULTANEOUS USE OF TWO RESPIRATION CHAMBERS WITH UNIVERSAL RESPIRATION APPARATUS.

Blower C draws air from respiration chamber A, passes it through sulphuric acid in container D, to remove water vapor, through soda-lime in container E<sub>1</sub>, to remove carbon dioxide, through sulphuric acid in container F<sub>1</sub>, to remove any water vapor given up by soda-lime, and back into respiration chamber A, the valves, V<sub>1</sub> to V<sub>4</sub>, inclusive, being turned in the proper direction. When valves are turned in reverse direction, chamber A is cut off from ventilating circuit and chamber B is connected with it. Blower C then draws the air out of chamber B, passes it through containers D, E<sub>2</sub>, and F<sub>2</sub>, containing sulphuric acid, soda-lime, and sulphuric acid, respectively, and returns it to chamber B. S<sub>1</sub> and S<sub>2</sub> are expansion chambers or spirometers for chambers A and B.

mal could be studied in a second chamber, and when it was necessary to ventilate this second chamber, a duplicate pair of valves could be turned on the universal respiration apparatus to divert the ventilating air current from the first to the second chamber and pass the outgoing chamber air through the second set of absorber bottles. This use of two chambers with one ventilating system was particularly successful when an exact measurement of the oxygen consumption was not desired, and it was quickly found

that with this particular set-up<sup>1</sup> the accurate measurement of the oxygen consumption of these animals was so difficult that for the most part such determinations were hardly worth while. Another advantage of this periodic ventilation is that the accumulation of water vapor inside the chamber reduces the amount of water vapor that can be given off by the animal and hence the rectal temperature of the animal can not fall appreciably below that of the environment. This is in line with the experiments of Krehl and Soetbeer,<sup>2</sup> who studied cold-blooded animals in saturated air.

*Measurement of water vapor*—In those experiments in which the excretion of water vapor was measured quantitatively an oil seal was used in the respiration chamber and spirometer. The circulation of air through the system was maintained throughout the entire experiment to absorb the water vapor, and the two Williams bottles of sulphuric acid preceding the soda-lime bottle were weighed both at the beginning and end of the period. It was disadvantageous to pass a large volume of air through the carbon-dioxide absorbing vessel and carry water over from it into the following sulphuric-acid bottle, and thus run the risk of diluting the acid and having water escape. The air current was therefore shunted for the greater part of the time around the carbon-dioxide absorbing system and only during the last 15 minutes of each experimental period was the air passed through the carbon-dioxide absorbent. Thus the carbon dioxide was quantitatively absorbed in the last 15 minutes. The rate of ventilation was, on the average, approximately 7 liters per minute when the air current was being bypassed and for 15 minutes, roughly speaking, 30 liters per minute. Thus the total ventilation in the last 15 minutes would be equal to several times the volume of air in the respiration chamber, making no allowance for the volume of the snake, and hence any condensation of water vapor inside the chamber would be prevented and the carbon-dioxide content of the air residual in the chamber would always be reduced to an insignificant amount. The duplication of results in various periods by this method shows an extraordinarily uniform production of carbon dioxide and makes this procedure thoroughly justifiable.

*Determination of environmental temperature inside respiration chamber during experiments*—As early as 1915 the problem as to what was the true environmental temperature in which these animals were living became an acute one. Several mercurial thermometers were used in different localities in the respiration chamber and air circuit. In addition, resistance thermometers and thermo-electric devices in connection with a potentiometer were employed. A most critical analysis of all these recorded temperatures was made in estimating the probable environmental temperatures recorded in the following pages. It can be seen, however, that even in the 1930 and 1931 studies this factor still presented a great deal of difficulty. In all these

<sup>1</sup> The Carpenter gas-analysis apparatus, enabling the determination of minute changes in composition of chamber air, had not been perfected for use at the time of our New York series of experiments. This gas-analysis apparatus was, however, used in our 1930 and 1931 experiments in Boston. (See pages 27 to 41.)

<sup>2</sup> Krehl, L., and F. Soetbeer, Arch. f. d. ges. Physiol., 1899, **77**, p. 629.

cases the chambers were hermetically sealed with a water seal. They were not calorimeters, but except for the 908-liter chamber, it was possible to heat them and regulate the temperature satisfactorily. In the case of the 908-liter chamber the temperature of the laboratory room sufficed for control, together with a moderate amount of protective blankets over the chamber. The particular feature of the combination of subsidiary chamber inside the larger chamber was a more perfect control of the environmental temperature at which these animals were studied.

*Alcohol check tests*—The accuracy of these respiration apparatus was frequently controlled by alcohol check tests, as is the custom of the Nutrition Laboratory. One desirable feature of the alcohol check test could not, however, be introduced. It is believed that ideally every respiration apparatus should be controlled by alcohol check tests, in which the amount of alcohol burned corresponds to the development of carbon dioxide and the absorption of oxygen under the conditions of experimenting in which the animal will be used. The difficulty of burning alcohol at a rate to produce as small an amount of carbon dioxide as that produced by the albino rat was great and was surmounted only after a long period of experimentation.<sup>1</sup> With these cold-blooded animals the carbon-dioxide production was even lower, and hence this desired ideal test was not attempted. We are convinced, however, that the apparatus functioned perfectly, that there could be no loss or gain of carbon dioxide in the system, and hence the results can be relied upon.

## RESPIRATION APPARATUS USED IN 1930 BOSTON EXPERIMENTS WITH TORTOISES

A seeming extraordinary diversity in the metabolism of tortoises as compared with the metabolism of the other cold-blooded animals measured in the experimental series of 1915-1921 was first brought out in the final calculation and assessment of values in the early stages of preparation of this report in the summer of 1930. This made it desirable to confirm, in part at least, the earlier observations on tortoises by further measurements.<sup>2</sup> Since 1921, when the research at New York stopped, there has been a material advancement in technique, particularly in the determination of the respiratory quotient, and with the Carpenter gas-analysis apparatus respiratory quotients can now be determined with a higher degree of accuracy than ever before. The respiratory quotients obtained by the technique employed in the New York series of observations we specifically disavow and hence shall not publish them, contenting ourselves with the statement that the respiratory quotient in general with our animals was essentially that corresponding to the combustion of fat. With the snakes, alligators and possibly the lizards this is perhaps a justifiable assumption, since they were living on animal food containing but a small amount of carbohydrate and the combustion must have been essentially that of a mix-

<sup>1</sup> Benedict, F. G., *Journal of Nutrition*, 1930, **3**, p. 173.

<sup>2</sup> In these later measurements, made in the fall of 1930, fundamental changes in the calculation of the surface area of the tortoise changed the picture materially. (See pages 338, 362 and 427.)

ture of fat and protein with the fat predominating, save in times of extreme fasting. Tortoises, on the contrary, are essentially vegetarians. It is possible that food may remain in the stomach of the tortoise for a long period. Hence the respiratory quotient may stay at a high level for a long time, and it would be uncertain when the real fasting or the real fat respiratory quo-

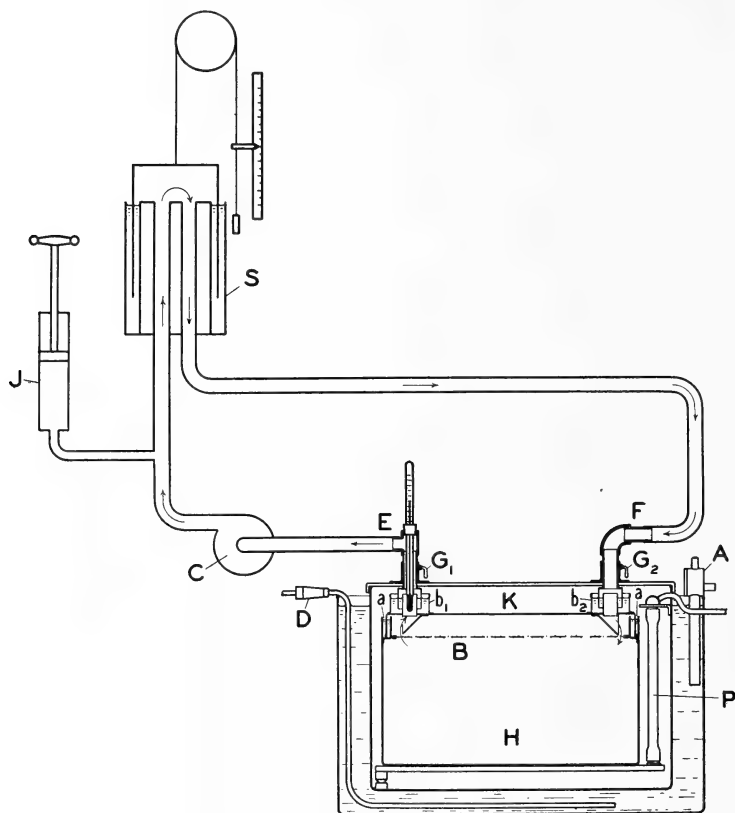


FIG. 8—SCHEMATIC OUTLINE OF RESPIRATION CHAMBER AND VENTILATING SYSTEM USED IN 1930 EXPERIMENTS WITH TORTOISES.

H, subsidiary 27-liter chamber with water seal, a, wire-mesh top, B, and cover, K. F, intake pipe and E, outlet pipe with water seals,  $b_1$  and  $b_2$ ; C, blower; S, spirometer; J, pump for sample of chamber air; P, pneumograph; D, electric heater; A, thermostat.

tient would be obtained. The paucity of information regarding the relative weight of shell and flesh of tortoises also made it desirable to study an animal that could subsequently be dissected.

Thanks to the courtesy of Dr. Raymond L. Ditmars, two South American gopher tortoises, weighing approximately 4 kg. each, were sent to the Nutrition Laboratory in the fall of 1930 for experimental purposes. These tortoises were usually fed bananas, with some lettuce. The respiratory exchange was studied in exactly the same respiration chamber as shown

in figure 2 (page 20), that is, the subsidiary 27-liter chamber inside the 85-liter chamber. The 27-liter chamber, H (fig. 8), is provided with a wire-mesh top, B, a cover, K, dipping into the water seal, a, and with tubes, E and F, conducting air out of and into the chamber. These tubes are likewise provided with water seals,  $b_1$  and  $b_2$ , so arranged as to insure flexibility for recording by means of the pneumograph, P, the degree of activity or the degree of repose of the tortoise. Control of the temperature inside the chamber is obtained by the electric heater, D, and the thermostat, A. Instead of attempting to absorb all the carbon dioxide, as in the earlier experiments, the chamber was used as a closed chamber apparatus and the carbon dioxide allowed to increase during the period from 0.03 per cent (the initial content of outdoor air) to approximately 1 or 1.25 per cent. The length of time for this increment was noted, and the percentage increase was multiplied by the total volume of the chamber (less volume of animal), accessory tubes and spirometer, to compute the total carbon-dioxide production.

At the beginning of the experiment, the animal is placed in the chamber and the chamber thoroughly ventilated by connecting the inlet pipe, F, directly with outdoor air. The outlet pipe, E, leads directly to a small rotary blower, C, which in turn drives the air into a 2.5 liter spirometer, S, in which a light, non-volatile oil is used as a liquid. The air leaving the spirometer either enters the room during the initial period, or during the actual time of experimenting is returned to the chamber, H. In the latter case the inlet pipe, F, is connected with the spirometer. The closed circuit therefore consists of the respiration chamber, H, the pipe, E, leading to the blower, the blower, C, the spirometer, S, and the return pipe, F, to the chamber. The volume of this apparatus obviously was constant in all the experiments, save for the two fluctuating values for the volume of the animal used and the level of the spirometer bell, which latter could be read on a millimeter scale. The carbon dioxide was thus allowed to accumulate and the oxygen deficit could be noted. At the end of the time when approximately a 1-per cent increment in carbon dioxide was expected, the air was rapidly circulated through the closed system for 5 minutes to insure uniformity, and then a sample was withdrawn for gas analysis in the pump, J.<sup>1</sup> Notes were also made at the end of the period regarding the level of the spirometer bell, the temperature of the water bath surrounding the 27-liter chamber, the temperature of the air leaving the chamber, and the atmospheric pressure. The apparatus was ventilated with outdoor air before each period, and the samples were always taken at the end of the period. The gas analyses were all made on the Carpenter gas-analysis apparatus,<sup>2</sup> usually either by E. L. Fox or by George Lee. This apparatus was used in

<sup>1</sup> The pump used has been described by Benedict, F. G., Boston Med. and Surg. Journ., 1927, **197**, p. 1161; *ibid.*, Chinese Journ. Physiol., Report Series No. 1, 1928, p. 39; *ibid.*, Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1929, Abt. IV, Teil 13, p. 1.

<sup>2</sup> Carpenter, T. M., Journ. Biol. Chem., 1923, **55**, p. xix; *ibid.*, Journ. Metab. Research, 1923, **4**, p. 1; Benedict, F. G., Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1924, Abt. IV, Teil 10, p. 628; Carpenter, T. M., and E. L. Fox, Journ. Biol. Chem., 1926, **70**, p. 115.



its latest modification and most efficient form, as recently described.<sup>1</sup> Assuming that the air is saturated with water vapor at the temperature of the apparatus, one can compute rapidly from the volume of the apparatus and the results of the gas analysis the carbon-dioxide production and the oxygen consumption of the tortoise during the period of measurement. On the Carpenter gas-analysis apparatus the percentage of carbon dioxide in a sample of air can be determined to within  $\pm 0.003$  per cent and the oxygen percentage can also be noted with an equally high degree of accuracy.

A typical calculation of the results of an experiment with this type of apparatus is given in table 1. The volume of the apparatus, as reported in this typical calculation, was determined by an exact calibration with a

TABLE 1—*Typical calculation of an experiment with a tortoise, using the respiration apparatus illustrated in figure 8.*

Oct. 14, 1930; tortoise A, 4252 gm.; rectal temp. 30.5° C. at 4<sup>h</sup>45<sup>m</sup> p.m.

Ventilation with outdoor air started at 4<sup>h</sup>55<sup>m</sup> p.m.

Barometer 761.3 mm.; temp. bar., 21.0° C.; corrected bar. 759 mm.

PERIOD I		
	Start 5 <sup>h</sup> 15 <sup>m</sup> p.m.	End 6 <sup>h</sup> 15 <sup>m</sup> p.m.
Temp. air line.....	28.30° C.	28.74° C.
Temp. bath.....	30.70° C.	30.70° C.
Sample drawn.....	6 <sup>h</sup> 15 <sup>m</sup> p.m.	
Spirometer level at time of calibration.....		mm. 132.2
Spirometer level at end of period.....		mm. 110.0
Difference .....		mm. -22.2
Volume of apparatus by calibration (spirometer level 132.2 mm.).....		l. 31.383
Volume of animal.....		l. 4.252
Difference .....		l. 27.131
Correction for difference in spirometer level (22.2 x .02132 <sup>2</sup> ).....		l. -.473
True volume of air in apparatus.....		l. 26.658
Volume at 0° C. (dry) and 760 mm. (26.658 x 0.868 <sup>2</sup> ).....		l. 23.139
CO <sub>2</sub> produced by tortoise (23.139 x .01186 <sup>3</sup> ).....		c.c. 274.4
O <sub>2</sub> consumed by tortoise (23.139 x .01468 <sup>3</sup> ).....		c.c. 339.7
R.Q. ....		0.81

<sup>1</sup> Each millimeter length of the spirometer bell corresponded to 21.32 c.c.

<sup>2</sup> Factor for reduction of saturated air in apparatus from 28.74° C. and 759 mm. to 0° C. (dry) and 760 mm. See Carpenter, T. M., Carnegie Inst. Wash. Pub. No. 303A, 1924, table 8.

<sup>3</sup> Per cent carbon-dioxide increment and oxygen deficit, as determined by gas analysis, corrected for CO<sub>2</sub> and O<sub>2</sub> in outdoor air entering chamber.

known amount of carbon dioxide. Although one could compute the volume of the apparatus with reasonable exactness from the measurements of the rectangular chamber, the size of the tubings and the volume of the spirometer, the volume was determined in a different way. The chamber with oil seal was connected with the blower and the spirometer as usual, and a sulphuric-acid bottle was placed between the exit tube of the chamber and

<sup>1</sup> Carpenter, T. M., R. C. Lee, and A. E. Finnerty, Wissensch. Arch. f. Landw., Abt. B., Tierernährung u. Tierzucht, 1930, 4, pp. 1-26.

the blower. The system was ventilated thoroughly until the air circulating through it was absolutely dry. There was then introduced through a tube leading to the base of the chamber one pumpful (370 c. c.) of dry carbon dioxide, the exact volume of which under standard conditions one could compute from the known temperature of the pump and the prevailing atmospheric pressure. The carbon-dioxide-enriched air was then carefully circulated throughout the system, this time without the sulphuric-acid bottle in the circuit, and after equilibrium was established a sample was taken for gas analysis and analyzed upon the Carpenter apparatus. From this analysis and from the initial volume of carbon dioxide introduced, the total volume of the circulating system was calculated from the equation: Total volume of system is to volume of pump at standard conditions as 100 per cent is to percentage of carbon dioxide in sample analyzed. On September 10, 1930, the volume of the apparatus was found to be 31.34 liters and on September 11 it was 31.42 liters.

By means of the water bath of the chamber, as shown in figure 8, the environmental temperature could be satisfactorily controlled, and experiments were made with temperatures as low as 14° C. and as high as 36° C. The use of the internal chamber likewise permitted the graphic record of activity, although in general the tortoises were quiet, particularly at the lower temperatures and when without food. With food and at the higher temperatures they were more inclined to be active. Experimenting in the evening did not materially better this condition, so it became at times essential, as it was in the earlier work, to watch the apparatus, make the reading for volume (level of spirometer bell), and draw a sample during the period when the repose was satisfactory.

Since the 27-liter respiration chamber was fairly large for the smaller of our two tortoises, a special metallic chamber was constructed of 16-liter capacity (fig. 9). This 16-liter chamber was placed inside the 85-liter chamber and was ventilated and used separately. It was not encased in wood and was not provided with a water seal, but was closed by a sheet of galvanized iron, well waxed into place by the ordinary physicist's wax.<sup>1</sup> The ingoing and outgoing air pipes (at the bottom and in the cover of the chamber, respectively) were then connected with the blower and the spirometer, and although the degree of flexibility of the activity recording system was thereby somewhat diminished, there never was doubt as to whether the animals were quiet or too active to be employed in the so-called "standard metabolism" measurements (see page 155). This chamber, having a smaller volume, made it possible for the periods of measurement to be somewhat shorter with the smaller tortoise, as it was not necessary to wait an undue length of time until the carbon-dioxide content of the chamber air increased to 1 per cent. The smaller tortoise was used in both the 27-liter and the 16-liter chamber. The results were essentially the same with both chambers.

During the course of the investigation in the fall of 1930 fluctuations in the respiratory quotient appeared that were so puzzling that one instinctively

<sup>1</sup>This physicist's wax consists of four parts beeswax and one part Venice turpentine (not synthetic), melted together.

wished it were possible to have a mask to put on over the head of the tortoise, that is, to reduce the extraneous volume to a minimum. This was impracticable, but a number of experiments were made with the following equipment. A rectangular, glass aquarium chamber, A, 20 cm. wide, 33 cm. deep, and 32 cm. long (internal measurements), was provided with a metallic cover, C, to which tubes were attached (fig. 10). The tortoise was

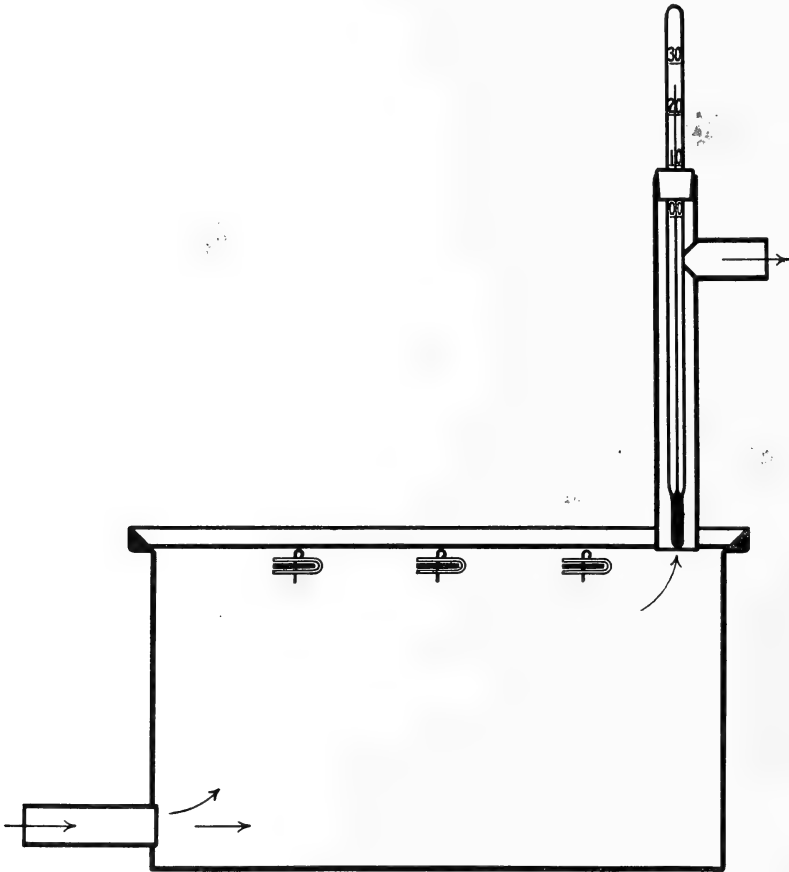


FIG. 9—RESPIRATION CHAMBER OF 16-LITER CAPACITY, USED IN STUDYING SMALL TORTOISES.

placed in this jar with water at the desired temperature, usually not far from 30° C. The animal floated with the head out of water, being usually fairly quiet, and when the metallic plate was waxed on the top of the jar there was a layer of air perhaps 20 mm. deep above the water. The cover was waxed in place by physicist's wax. Outdoor air was led into the apparatus by the blower, B, the rotamesser, R, indicating the rate of ventilation. By thus introducing air into the jar at the rear of the animal and drawing it out near the head, we hoped to be able to sweep out the carbon dioxide fairly

rapidly with a continuous ventilating air current. For this purpose a slow rate of ventilation was sufficient. The outgoing air was collected in a 6-liter spirometer, S, the volume collected was read by noting the change in level of the spirometer bell, and then a sample was taken therefrom for analysis in the pump, G. A thermometer, T, was inserted through the cover, C, into the air above the water in the aquarium jar. This form of apparatus was used primarily to study any seeming rapid transitions in the

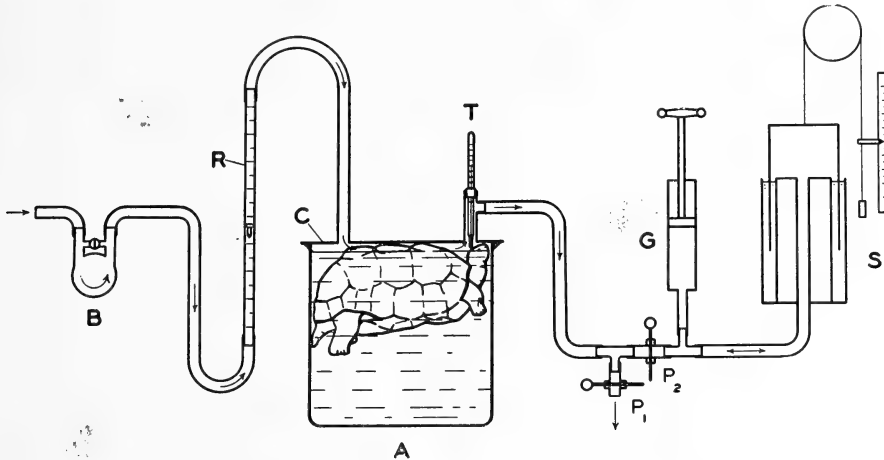


FIG. 10—AQUARIUM CHAMBER FOR TORTOISE.

A, glass aquarium with metallic cover, C; B, blower; R, rotameter; T, thermometer; G, pump for withdrawing sample of air for gas analysis; S, spirometer; P<sub>1</sub> and P<sub>2</sub>, spring pinchclamps to direct outgoing chamber air either into the laboratory room or into the spirometer, S.

respiratory quotient. The animal was not as tranquil when in the water as when in the metallic chamber. Even when temperature conditions were the same the metabolism measurements were always somewhat higher when the tortoise was immersed in the water in the aquarium than when in air inside the respiration chamber.

### RESPIRATION APPARATUS USED IN 1931 BOSTON EXPERIMENTS WITH A PYTHON

Analysis of the metabolism observations obtained upon snakes in the New York series indicated that there were some lacunæ in the data that should be filled in before publication. Furthermore, as with the tortoise, it seemed desirable to control the measurements on snakes in the New York series by observations on a large snake with even more modern technique, particularly a technique that would permit the accurate determination of the respiratory quotient. At the conclusion of the 1930 tortoise series, therefore, arrangements were made to secure a python, and fortunately it was possible for the measurements to be made by the same operator, E. L. Fox, who had assisted in the New York observations and in the Boston observations on the tortoise. Since it was desired to study the temperature relations

between the animal and the environment, particularly during digestion, one objective was to secure a snake that would feed and thus permit the study of certain phases of the digestive cycle. Dr. Ditmars of the New York Zoological Park kindly purchased a "*Python molurus*" for the Nutrition Laboratory. It was taken to the Park and there kept for several days. Food was offered to it, which it readily ate. Observations on its rectal temperature compared with the environmental temperature were made at that time, and on January 9, 1931, the python was brought to Boston. But perhaps the most important feature of the work with this python was the measurement of the respiratory exchange, with special emphasis upon the respiratory quotient. These measurements greatly illuminated the whole picture regarding the physiology of snakes, although bringing to light some extraordinarily complicated and thus far inexplicable facts.

The techniques employed varied in accordance with the special object of the measurements, but were not fundamentally different from many others employed in the Nutrition Laboratory. The variations were introduced to secure the greatest accuracy in the determination of the respiratory quotient, to measure the water vapor quantitatively, and to contribute especially to the study of the difference between the cell temperature and the environmental temperature of the animal. In all the techniques the galvanized iron box in which the snake rested was placed inside the water-jacketed chamber shown in figure 1 (page 18), because the temperature of this water-jacketed chamber could be regulated so that it would be as low as 14° or as high as 38° or higher, either by adding ice to the water bath or by heating the water with an electric heater controlled by a thermostat. Two different sized boxes were used, according to experimental conditions, with the object of having the volume of extraneous air about the snake commensurate with the production of carbon dioxide and the absorption of oxygen. At the low temperatures, when the metabolism was very low, a box was used of a size that would reduce the air about the animal as much as possible, thus resulting in a higher percentage of carbon dioxide in the air remaining in the box or coming from the box. On the other hand, at the high temperatures it was disadvantageous to crowd the animal into such a small space and possibly hinder its normally larger heat loss. Hence a larger box was used at the higher temperatures. Both boxes were of galvanized iron, constructed much like the 16-liter box used for tortoises (fig. 9, page 32), with ingoing and outgoing air pipes in the bottom and cover, respectively, the cover being sealed air-tight with physieist's wax. The rate of ventilation of the apparatus was likewise determined by the magnitude of the production of carbon dioxide and the absorption of oxygen, and furthermore by the desirability of maintaining a fairly low humidity in the chamber air. Hence changes in the ventilation rate and in the type of rotary blower employed were necessitated, and on occasions supplementary ventilation was installed.

When small amounts of carbon dioxide were produced, that is, at the low temperatures, the closed-circuit principle was employed. At the higher temperatures, when the metabolism was more rapid, the open-circuit principle was used. In some instances the air leaving the respiration chamber

was allowed for the greater part of the time to escape into the laboratory room. At intervals, during short periods of from 3 to 4 minutes, the air was collected and measured in a spirometer. A sample of the air in the spirometer was then analyzed, and the gas-analysis determinations were applied to the total volume of air collected in the spirometer. In other instances most of the air leaving the chamber was passed through a wet gas meter and a continuous aliquot sample was forced through a fine jet

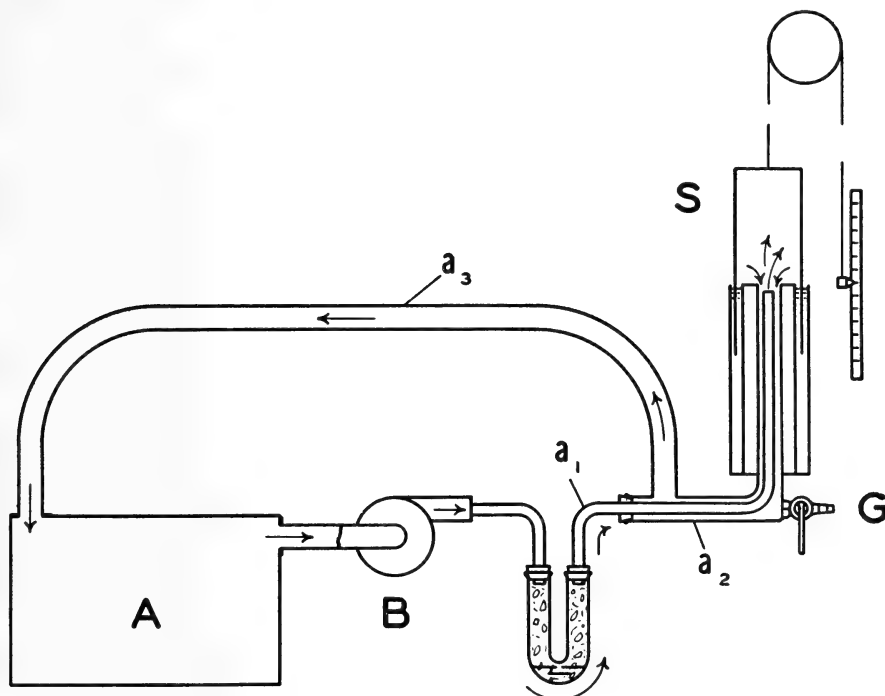


FIG. 11—CLOSED-CIRCUIT RESPIRATION APPARATUS FOR MEASUREMENT OF GASEOUS METABOLISM OF THE 1931 PYTHON AT LOW TEMPERATURES.

Air from chamber, A, is withdrawn by blower, B, passed through a U-tube of sulphuric acid where the water vapor is removed, through the tube,  $a_1$ , and into the spirometer, S. It leaves spirometer through tubes,  $a_2$  and  $a_3$ , and returns to chamber. A sample of air in the closed system is withdrawn through cock, G, for gas analysis.

into the spirometer, at one side. This sample was ultimately analyzed, and the results were applied to the readings on the gas meter.

#### CLOSED-CIRCUIT PRINCIPLE

The main features of the closed-circuit principle are shown in figure 11. Air is withdrawn from the box or respiration chamber, A (in which the snake is placed), by a blower, B, and passed through a U-tube containing sulphuric acid. It is then discharged through a tube,  $a_1$ , into the bell of a small spirometer, S. The air leaves the spirometer through the tube,  $a_2$ , and the side tube,  $a_3$ , and returns to the respiration chamber, passing on

its way through a rotamesser<sup>1</sup> (not shown in figure 11). This rotamesser is used simply to indicate the rate of ventilation. With the apparatus as thus set up, the air can be completely circulated through the system at any desired rate. The spirometer has an oil seal. The total water vaporized is absorbed and weighed in sulphuric acid in the U-tube, and hence the snake is in a closed volume of dry air. A sample of the air in the closed system is drawn through the cock, G, at the end of the experimental period and analyzed. The composition of the air in this system at the start of an experiment was considered to be the same as that of outdoor air, since the apparatus was thoroughly ventilated with dry outdoor air before the experiment began. For this preliminary sweeping out, the system was used as an open circuit and the outdoor air was passed through two calcium-chloride vessels before it entered the respiration chamber. To be sure, the snake was continually adding a small amount of carbon dioxide to the air, but because of the rapid rate of ventilation used it can be assumed that the carbon-dioxide content at the start of the metabolism measurements was essentially that of outdoor air. This fact was checked by gas analysis on several occasions and found to be not far from correct. When the respiration experiment proper was to begin, the circuit was closed.

The volume of this closed circuit was calibrated as follows. The system, including the empty box without the snake, was first thoroughly ventilated with outdoor air. Half a pumpful<sup>2</sup> (about 185 c.c.) of pure, dry carbon dioxide was then introduced, the air inside was next thoroughly mixed by the blower, and a sample was taken for gas analysis. The true volume (at 0° C., dry, and 760 mm.) of the closed circuit, including not only the respiration chamber but the blower, the U-tube, the spirometer bell at a given level, and the rubber tubing, was then computed by proportion, the ratio between the volume of the half pumpful and the volume of the system being considered to be the same as the ratio between the percentage of carbon dioxide in the system after the introduction of the half pumpful of carbon dioxide (less the percentage of carbon dioxide in outdoor air) and 100 per cent. This calibration showed that the volume of the closed system was 21.4 liters when the larger sized snake box was used, and 13.8 liters when the smaller box was used. With the smaller box it was possible to obtain a somewhat higher percentage of carbon dioxide in the air inside the system within a reasonable length of time.

#### OPEN-CIRCUIT PRINCIPLE

Since at the higher temperatures the amount of carbon dioxide produced by the snake and accumulated in the closed-circuit apparatus was so great that the analysis of a sample of the chamber air gave a reading for carbon dioxide that was frequently "off scale" on the gas-analysis burette,

<sup>1</sup>The rotamesser, although a relatively old instrument, has only recently been used in the Nutrition Laboratory. In our experience it is exceeded by no other instrument for measuring air flow. It is furnished, unfortunately at a very high price, by the Deutsche Rotawerke, Aachen, Germany.

<sup>2</sup>See page 29.

the open-circuit principle was used when studying the python at the higher temperatures. For this purpose the snake box, A, inside the 85-liter chamber shown in figure 1 (page 18) is supplied with dry outdoor air. A blower, B (fig. 12), withdraws the air from the chamber and passes it through sulphuric acid in a U-tube, and then through a rotameter (not shown in figure 12) so that the approximate rate of ventilation is indicated. The air then for the most part is discharged into the laboratory

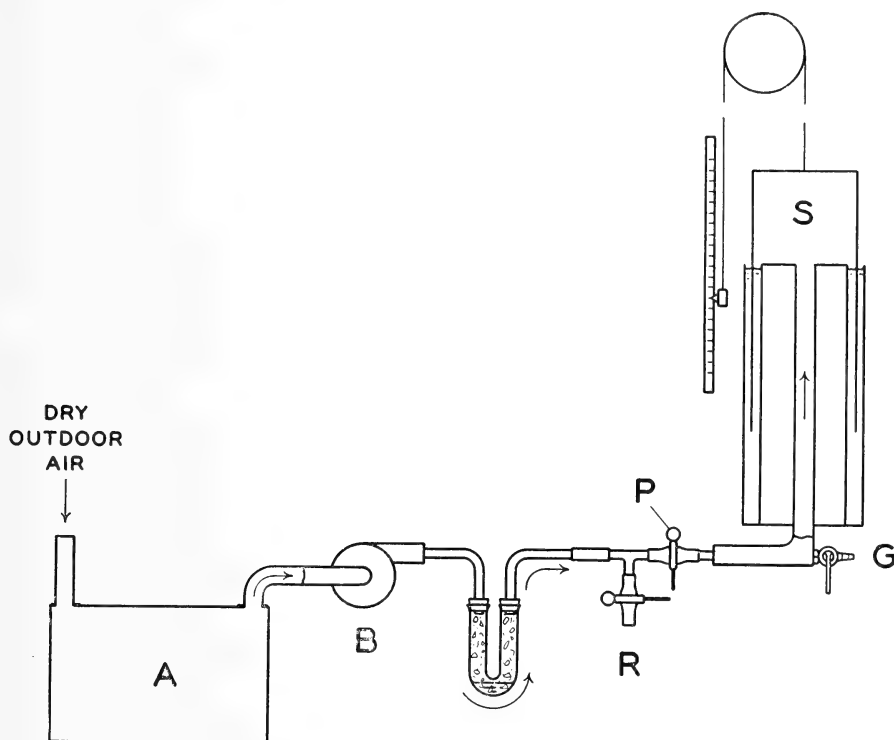


FIG. 12—OPEN-CIRCUIT RESPIRATION APPARATUS FOR MEASUREMENT OF GASEOUS METABOLISM OF 1931 PYTHON AT HIGH TEMPERATURES, IN SHORT, INTERMITTENT PERIODS.

Air from chamber, A, is withdrawn by blower, B, passed through sulphuric acid in U-tube, and discharged into laboratory room through tube, R. At intervals tube, R, is closed, pinchclamp, P, is opened, and chamber air is collected in spirometer, S. A sample for gas analysis is taken through cock, G.

room through the tube, R. At selected periods of from 3 to 4 minutes, depending upon the rate of flow of the air from the chamber, the air is discharged not into the room but into a 6-liter spirometer, S, by closing cock, R, and opening pinchclamp, P. Thus all the air from the chamber is not collected, but only a portion of it from time to time. When the spirometer is filled, the outgoing air current is deflected into the room again, the change in level of the spirometer bell is recorded, and a sample of air is withdrawn from the spirometer through the cock, G. Obviously before taking the sample, all the tubes and connections and the dead space in the spirometer are washed out by partly filling the spirometer with



chamber air two or three times. With this type of apparatus the measurement of the respiratory exchange was limited to short periods of from 2 to 4 minutes, the time required to fill the 6-liter spirometer. In some instances when this particular set-up was employed, the outdoor air was not dried before being introduced into the chamber and hence the carbon-dioxide production and the oxygen consumption alone were determined and

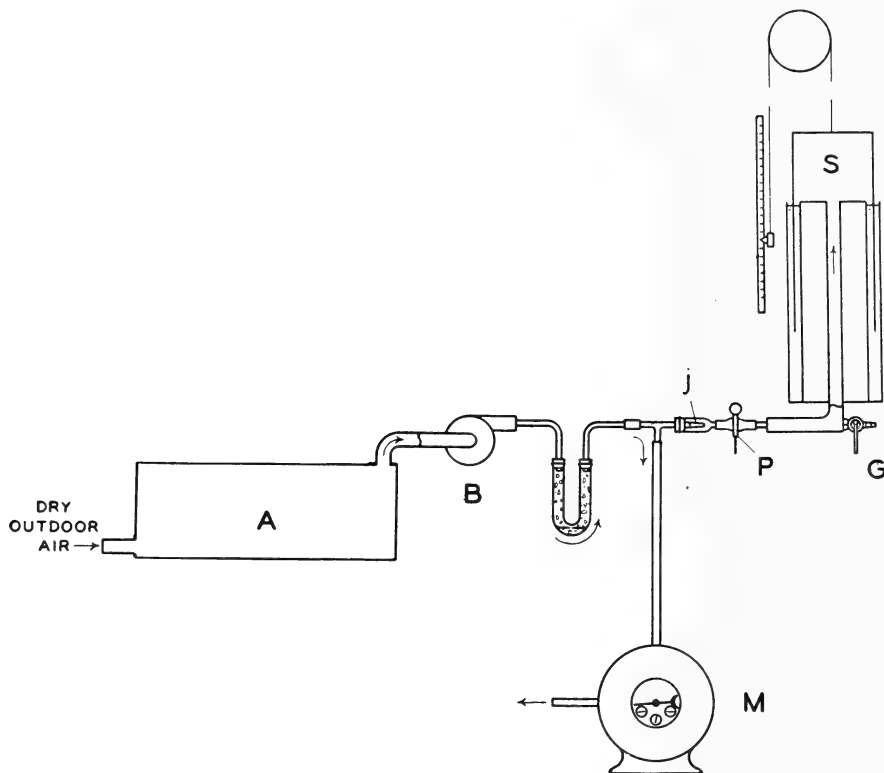


FIG. 13—OPEN-CIRCUIT RESPIRATION APPARATUS FOR CONTINUOUS MEASUREMENT OF GASEOUS METABOLISM OF 1931 PYTHON AT LOW AND HIGH TEMPERATURES.

Air from chamber, A, is withdrawn by blower, B, passed through sulphuric acid in the U-tube, through the wet gas meter, M, and discharged into laboratory room. Simultaneously a small portion of air escapes through jet, j, and is collected in the spirometer, S. A sample for gas analysis is withdrawn through cock, G, pinchclamp, P, momentarily cutting off connection between spirometer and rest of system.

no attempt was made to measure the water vapor given off by the animal. When dry outdoor air was introduced, the water vaporized by the snake was measured by the change in weight of the U-tube of sulphuric acid. Thus it was possible to absorb all the water vapor given off by the snake during the entire period of observation and at the same time measure the respiratory gases only for short periods, by deflecting the air momentarily into the spirometer.

In some experiments the open-circuit principle was also used to measure the entire carbon-dioxide production and oxygen consumption during the

experiment, by metering all the air leaving the chamber, securing an aliquot sample, and analyzing that (fig. 13). Dry outdoor air was led into the chamber as before. The air was withdrawn from the chamber, A, by a blower, B, passed through a U-tube of sulphuric acid, through a rotamesser (not shown), and finally through a calibrated, 1-liter wet gas meter, M, of the American Meter Company. To secure an aliquot sample, use was made of a jet such as has been employed in the Nutrition Laboratory for some time. The air was not allowed to enter the spirometer, S, at full speed so as to fill it in three or four minutes, but a small jet, j, with a fine hole in the center of it (the equivalent of a No. 65 drill with a diameter of 0.9 mm.) was placed at the entrance to the spirometer. Thus a continuous flow of air entered the spirometer at a slow rate and at the same time the main volume of outgoing chamber air was metered on the wet gas meter. A sample of the chamber air collected in the spirometer was withdrawn through the cock, G, to be analyzed, the spirometer being cut off from the rest of the system at the time by means of the pinchclamp, P. The total volume of outgoing air was thus the sum of the volume recorded on the gas meter and the volume collected in the spirometer. To this volume (reduced to 0° C., dry, and 760 mm.) the results of the gas analysis of the aliquot sample were applied, to compute the total carbon-dioxide production and the total oxygen consumption. With this open-circuit arrangement, as shown in figure 13, the larger snake box was used for the experiments at the higher temperatures and the smaller box for the experiments at the low temperatures. The total ventilation of the chamber was regulated so that the carbon dioxide in the air leaving the chamber would not be greater than 1 per cent. The carbon-dioxide content of the air in the open system was assumed to be constant during the periods of measurement, and no correction in the results was made for change in residual carbon dioxide. This was believed to be consistent, since the period values always showed good agreement and the ventilation rate was sufficiently high to maintain a uniform percentage of carbon dioxide in the air remaining inside the chamber.

In the belief that, at the high temperatures, the humidity inside the closed circuit shown in figure 11 would not be low enough to permit the snake to lose heat properly by vaporization of water, even though the air entering the chamber was dried by passing it over calcium chloride, a supplementary ventilation of the open circuit was used at the higher temperatures, much as was employed in the closed-circuit apparatus. The arrangement with supplementary ventilation is shown in figure 14. The blower, B<sub>1</sub>, draws the air from the chamber, A, forces it through sulphuric acid in the U-tube, through the rotamesser (not shown), and back into the chamber. Thus the water vapor is removed from the air current, but not the carbon dioxide. A second blower, B<sub>2</sub>, simultaneously removes air from the chamber, discharges the greater part of it into a wet gas meter, M, a small fraction passing through the jet, j, into the spirometer, S, as before. A sample for gas analysis is withdrawn from the spirometer through the cock, G, the pinchclamp, P, serving to cut off the rest of the

system momentarily. The rate of ventilation of blower,  $B_1$ , was very high so that the humidity was kept low. This equipment with the supplementary ventilation for reduction of the humidity was used in most of the experiments at the higher temperatures.

It was thought that when the snake was resting in the galvanized iron box, the ventilation over the animal might be somewhat restricted, since

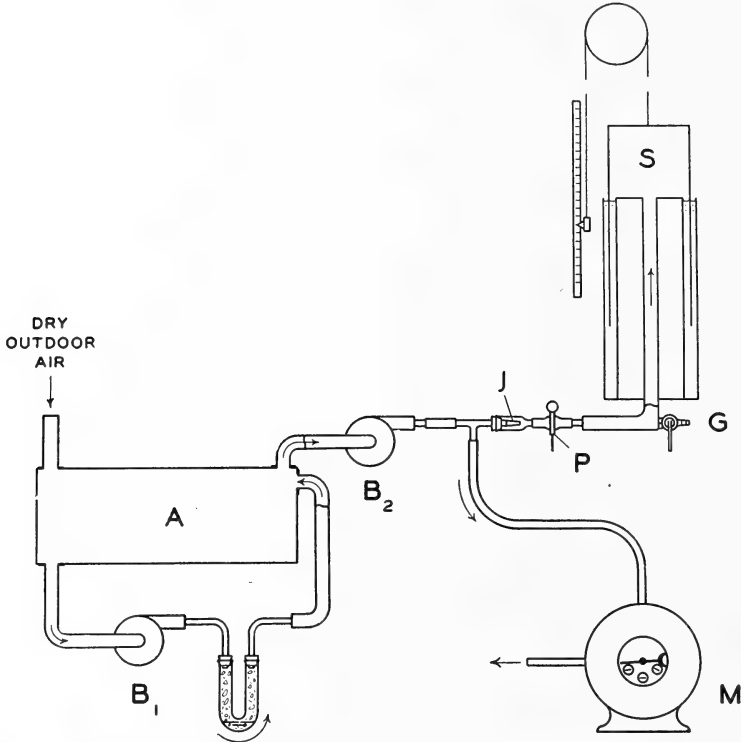


FIG. 14—OPEN-CIRCUIT RESPIRATION APPARATUS FOR CONTINUOUS MEASUREMENT OF GASEOUS METABOLISM OF 1931 PYTHON AT HIGH TEMPERATURES WITH SUPPLEMENTARY VENTILATION FOR REDUCTION OF HUMIDITY.

Air from chamber, A, is withdrawn by blower,  $B_1$ , passed through U-tube of sulphuric acid, and returned to chamber. Blower,  $B_2$ , simultaneously removes air from chamber and discharges most of it through wet gas meter, M. Part of air continually escapes through jet, J, into spirometer, S. A sample for gas analysis is withdrawn through cock, G, the pinchclamp, P, being closed to shut off connection between spirometer and rest of system.

a considerable portion of its surface area might not come in contact at all with the moving air. To avoid this difficulty, in so far as possible, a false wire floor was placed in the bottom of each of the boxes so that the air entering at the bottom of the box might filter up through the snake, so to speak, and leave at the top. On the supposition that it was still more desirable to arrange the folds of the snake so as to have as little actual coiling as possible, a special cage was used inside the larger of the galvanized iron boxes, in one experiment (January 24). This was a wire-

mesh cage with three partitions so arranged as to represent almost a maze. The python was placed in this cage, partitions serving to separate the coils, and thus the largest possible surface area was exposed to the ventilating air current. A photograph of the python in this cage is shown in figure 15.

#### GAS ANALYSIS

It is obvious that no matter which of the techniques just described was used, the success of all the experiments depended upon the possibility of making an accurate gas analysis of an air mixture containing a small amount of carbon dioxide (about 1.0 per cent) and having a small oxygen deficit. Fortunately, with the Carpenter gas-analysis apparatus such accu-

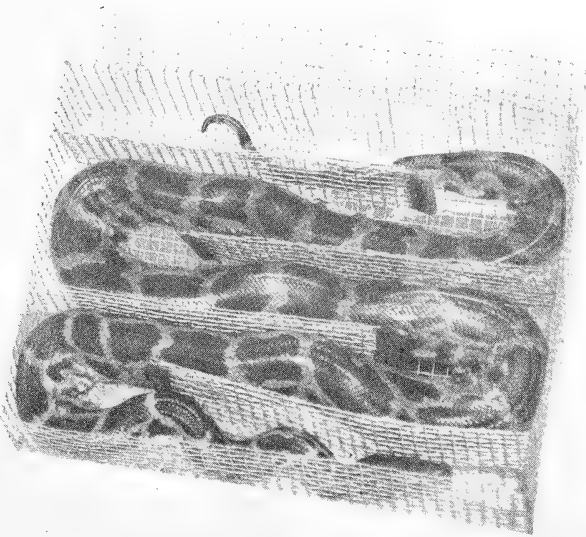


FIG. 15—WIRE-MESH CAGE WITH PARTITIONS. TO SEPARATE COILS OF SNAKE AND EXPOSE AS MUCH OF ITS SURFACE AS POSSIBLE TO AIR.

racy could be secured, and the entire research during 1930 and 1931 was made possible by the use of this apparatus.

#### GRAPHIC RECORD OF ACTIVITY

At first thought it would seem nonsense to attempt to register the activity of an animal that ordinarily lies as quietly as the snake. One has but to observe these large pythons in a zoological park to see that for hours at a time they remain almost motionless. It was found, however, that, especially at the higher temperatures, there was a distinct tendency for movement, although usually slow. Hence in every respiration experiment made with the 1931 python a graphic record of the degree of repose was

obtained, and it was found that when there were any movements of the snake, the center of gravity of the respiration chamber was only slowly but nevertheless positively changed. In the majority of the experimental periods practically no movements were registered, but when activity was noted, the record was of invaluable aid in interpreting the metabolism results. Particularly was this true when the python was inside the differential calorimeter (see page 425), for at a period when an attempt was being made to balance the electrical bridges, there was such a marked change in the heat production that the operator was at a loss to know what was the trouble until he examined the kymograph record and found that the snake had been moving.

At one time the Nutrition Laboratory was inclined to minimize the importance of graphic records of activity, but from our experience with this python we are now convinced that all respiration experiments should be accompanied by activity records. It is furthermore clear that, although these cold-blooded animals move slowly, whatever movement they do make has a much greater effect percentagewise upon the metabolism than do similar movements of a warm-blooded animal. In general one might say that muscular effort requires the same amount of energy in the cold-blooded animal as it does in the warm-blooded animal, and this results in increased heat. If the baseline metabolism is very low, as it is with the cold-blooded animal, obviously the extra energy needs for movement represent a much larger proportion of the basal needs than would be the case if the baseline were higher, as with the warm-blooded animal.

### RESPIRATION CALORIMETER

In some experiments carried out in Boston in 1920 on a boa constrictor and in two experiments with the python studied in Boston in 1931, attempts were made to measure the heat production directly by placing the snake inside an electrical compensation or emission calorimeter. This calorimeter has already been briefly described<sup>1</sup> and a complete description is being prepared for publication at the present time. The apparatus consisted of a closed chamber ventilated by a universal respiration apparatus, with an electrical equipment for the measurement of the heat production. By means of this calorimeter the belief was confirmed that the entire heat loss of a snake at the usual room temperature takes place by vaporization of water and that under many conditions heat is actually absorbed from the environment by the snake.

### BODY TEMPERATURE MEASUREMENTS

The relationship between the temperature of the cells and the heat production in warm-blooded animals, as shown by the increased metabolism during fever and muscular work and by the decreased metabolism during hibernation, profound undernutrition, and starvation, together with the well-known fact that with cold-blooded animals the metabolism is markedly af-

<sup>1</sup>Benedict, F. G., Boston Med. and Surg. Journ., 1925, 193, p. 807; *ibid.*, Bull. Soc. Sci. d'Hygiène Aliment., 1927, 15, p. 172.

feeted by the environmental temperature, made body-temperature measurements of prime importance. With the snakes and two of the tortoises, the temperature in the rectum was frequently recorded. Occasionally with the 5-meter python the mouth and the rectal temperature could be taken. When practical, sensitive mercurial thermometers calibrated with a standard Richter thermometer were employed for these observations. These could be read accurately to  $0.1^{\circ}$  C. and estimated to  $0.01^{\circ}$  C. The thermometer was held in place until the mercury did not show any change. The snakes did not resent this procedure appreciably. Indeed, on one day when the rectal temperature of the 1931 python was determined, the snake lay quietly in its cage with the thermometer inserted in the cloaca for an hour, and the rectal temperature could be read as desired, without any disposition on the part of the python to pull away from the thermometer. It was found that with the very small differential between the environmental temperature and the rectal temperature of the snake, a technical error might easily be introduced when the thermometer was brought out of a room having a temperature materially lower or higher than that of the snake itself. It became necessary, therefore, to warm or cool the thermometer approximately to the temperature of the snake before inserting it.

In measuring the rectal temperature of the snakes in New York, the animal was at first removed from the respiration chamber at the end of an experiment and exposed to the room air. This operation took at least two minutes. Subsequently, to avoid handling the animal and subjecting it to a change in temperature, the rectal temperature was measured at the end of an experiment by pulling the snake's tail out from the top of the chamber and the greater part of the body remained in the chamber undisturbed. This latter procedure was followed likewise in the case of the 1931 python.

*Thermo-electric body temperature measurements*—The measurements with the mercurial thermometer were frequently compared with measurements made by thermo-electric couples<sup>1</sup> inserted in the cloaca, particularly during the series of experiments carried out in Boston on boa N. But the special use of the thermo-electric method was to measure the skin temperature. These records of skin temperature were secured in a number of ways, by using thermo-electric junctions or needles laid upon the skin. Occasionally the pyrovolter, a modified potentiometer, was employed, but in our most extensive study of skin temperature the device described by Benedict, Coropatchinsky and Finn<sup>2</sup> was used. In the earlier studies of

<sup>1</sup> Although most of these measurements of rectal temperature with our animals were made with mercurial thermometers, the importance of using a rapid method, particularly the thermo-electric, soon became apparent. Nobili and Melloni (Ann. de Phys. et Chim., 1831, **48**, p. 198) first used the thermo-electric method to study the temperature of cold-blooded animals. Lombard (New York Med. Journ., January 1866, p. 241) used a similar method and points out with striking clearness the difficulties involved in this type of temperature measurement. Although he did not work with vertebrates, he noticed frequently that the temperature of the animals was lower than that of the air.

<sup>2</sup> Benedict, F. G., V. Coropatchinsky, and M. D. Finn, Journ. de Physiol. et de Path. gén., 1928, **26**, p. 1; *ibid.*, Leopoldina (Amerikaband), Berichte d. kaiserl. Leopoldinischen Deutsch. Akad. d. Naturforscher zu Halle, 1929, **4**, p. 129. (In English.)

the skin temperature of these cold-blooded animals at the New York Zoological Park the junctions were connected with a small d'Arsonval galvanometer, and the application junction was tied to a long bamboo pole, which could be inserted in the snake den and gently placed between the folds of one of the larger pythons (fig. 16). The skin temperature in this way could be readily and rapidly measured. Likewise by moving the junction around in the air, one could have a quick indication of the environmental temperature and the temperature of the graveled bed at the bottom of the den, on which the snake rested. With this electrical



FIG. 16—MEASUREMENT OF SKIN TEMPERATURE OF A SNAKE BY MEANS OF A THERMO-JUNCTION ATTACHED TO A LONG POLE.

device for skin-temperature measurements, particularly in the later experiments in Boston, it was possible to demonstrate the extraordinary relationship between the skin, the rectal and the environmental temperature of these large cold-blooded animals.

In the 1931 observations on the python, the skin-temperature apparatus was kept in the same room with the snake, and hence it was possible to measure the skin temperature at many different parts of the body and as frequently as desired. This was particularly helpful in studying the skin temperature following the ingestion of food. Thus, after the 1931 python had eaten two guinea-pigs, its body was greatly enlarged where the bodies of the guinea-pigs rested. The question arose as to whether there was any local heat due to digestive activity at this point. This question was studied by moving the thermo-junction over this part of the body and comparing the skin temperatures over the lump with the skin temperatures at other parts of the body (see page 83).

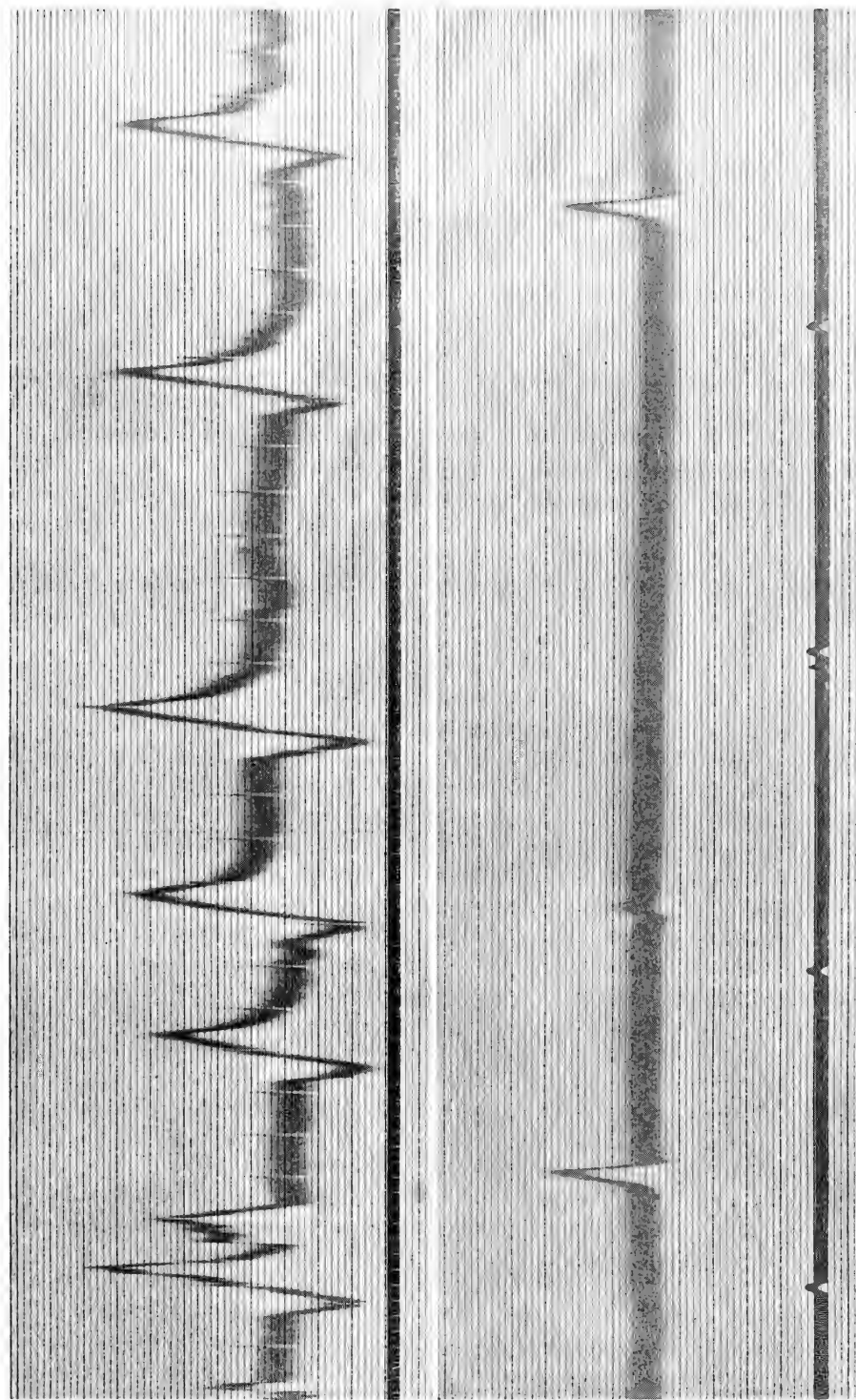


FIG. 17—TYPICAL ELECTROCARDIOGRAMS OF A TORTOISE.

Upper curve shows effect of activity upon heart rate. Lower curve was obtained when tortoise was quiet. Time is in seconds, time intervals being wider in lower than in upper curve because more rapidly moving paper was used.



### MEASUREMENT OF HEART RATE OF TORTOISE

The profound changes in metabolism noted with these cold-blooded animals at different temperatures made it highly desirable to secure, if possible, some indication of the heart rate. At the time of our New York series of measurements it was out of the question for us to attempt to determine the heart rate of any of the animals studied. But in 1930 when the two gopher tortoises were sent from the New York Zoological Park to the Nutrition Laboratory, there was available a fine Hindle string galvanometer with which records were taken by the physicist of the Nutrition Laboratory, V. Coropatchinsky. The intensely dry and non-conductive character of the skin or hide of the tortoise leg made the attachment of electrodes somewhat difficult, but after a little experience the electrodes were attached, frequently retained in place for some time, and the electrocardiograms were secured. In most of the observations made, simply the heart rate itself was recorded by noting on a slowly moving paper the number of the major impulses. In a few cases the rapidity of the moving paper was increased to obtain the picture for the entire heart cycle. Our first experiments were made with the Cambridge string galvanometer, for the heart action of the tortoise under ordinary temperatures and with special feeding was strong enough to record with this instrument. At lower temperatures, however, the Cambridge string galvanometer was not sufficiently sensitive; hence the Hindle instrument with a 6000 ohm string was used, and this gave perfect satisfaction. In figure 17 are shown two electrocardiograms of a tortoise, obtained with the Hindle galvanometer. These were secured by attaching electrodes preferably under the left front leg, near the body, and under the diagonally opposite rear leg. The upper electrocardiogram in figure 17 shows the effect of major muscular movements upon the heart rate and the general wandering of the string. The lower electrocardiogram was obtained with rapidly moving film when the tortoise was quiet. The time in seconds is indicated by the breaks in the heavy straight line below each curve.

### MEASUREMENT OF INSENSIBLE PERSPIRATION OF TORTOISE AND PYTHON

The insensible perspiration of the two tortoises used in the 1930 series and the python studied in 1931 was determined in a number of instances. The animal was weighed on a Sauter balance of the so-called "10-kg." size. This balance is sensitive to within 10 mg. and enables extremely accurate measurements. The tortoise was placed directly on one of the balance pans. The python was suspended on the balance in various types of box, always, however, with a natural ventilation that would insure the carrying off of what small amounts of water vapor were produced. In some cases the python was suspended in a woven wire-mesh box, which would permit the greatest exposure of its body surface. In other cases an electric fan blew air over the entire body. Occasionally at night the draft from the electric fan was directed into a funnel, which in turn conducted air to the bottom of the respiration box in which the snake was confined,

and the air left the box at the top. Usually the snake was surrounded by a rapid circulation of air at the humidity prevailing at the time.

### HANDLING OF ANIMALS

At the start of the experimental series in New York the snake was placed in the 85-liter or 75-liter box directly on the movable floor suspended by knife-edges and the spiral spring. Subsequently it was placed in a cage with metal walls and wire-mesh top, and this cage rested on the movable floor of the prevailing chamber. Because of the numerous folds of the snake, one could never be sure how much surface area was exposed to the environment. The contact of the body of the snake with the metallic walls of the chamber or cage reduced perceptibly the direct area for vaporization of water from the skin, but the tendency for these cold-blooded animals to approximate closely the environmental temperature reduced to a minimum the question of the surface area exposed in the folds. Experiments were made later in the New York series in which the snake was placed in the chamber inside a cage, the sides of which as well as the top were of wire gauze, so that vaporization could take place from all the folds that were not in contact with the snake itself. When the subsidiary 27-liter chamber was used, the snake was not put into a cage but was placed directly in the chamber, and the chamber was provided with an inner wire-mesh cover which could be clipped into place so that, if the outer cover (K, fig. 2) was lifted off, the animal could not escape.

The animal to be studied was first weighed and then usually placed in the respiration chamber several hours preceding the metabolism experiment, so that it might recover from the effects of handling and become adjusted to the environmental temperature at which it was to be measured. At the end of a series of measurements the animal was again weighed and returned to the reptile house, where it might have access to food and water.

Continuous measurements were made on the animal while inside the respiration chamber, extending from 1 or 2 days to 5 or 6 weeks, according to the type of observation made.

The python studied in 1931 was kept in a small room next to the laboratory containing the respiration apparatus, when metabolism measurements were not being made. But in many instances it remained inside the respiration chamber overnight, and the chamber temperature was controlled by the insulated water bath. During the intervals between the respiration experiments the snake was placed in a regular Abderhalden metabolism cage, but the wire grid around the top was reenforced with half-inch (12 mm.) mesh so that it was impossible for the snake to get its head out between the vertical wire bars. This cage proved to be particularly helpful, for it enabled the separation of the urine from the feces on several occasions and facilitated the handling of the animal. The bottom of the cage, which consists of a number of metallic bars, was nearly covered with a thin piece of wood and the snake was inclined to lie on this board rather than on the metallic bars, which possibly conducted

heat away from its body a little more rapidly than was to its liking. The temperature of the small room was controlled by means of the windows, the radiator and an electric fan. The radiating area of the radiator was altered as desired by covering it with different sized shields. The windows were opened or closed as much as needed, and an electric fan with an electric thermostat was arranged so that an electric contact could be made when the temperature of the room fell to a certain point and the contact could be broken when the temperature rose to the desired level. A standard, engineering, recording thermometer was used, and a complete record of the environmental temperature of the small room in which the python was kept when not in the respiration chamber was obtained throughout the entire period of experimentation. The environmental temperature was usually not far from 30°, but at times was purposely as low as 18°. In spite of this temperature regulation, however, there was one occasion when the temperature for a short time fell to as low as 12° and there were one or two occasions when it rose to 38°. The actual environmental temperature obtaining inside the respiration chamber during the metabolism measurements is shown in the tabulated data for this python. (See table 55, page 208.) The records of the temperature in the small room are of advantage in showing exactly the temperature conditions under which the snake had been living for 24 hours or more prior to each individual experiment, and will be referred to in the subsequent discussion.

## PHYSIOLOGY OF LARGE SNAKES

### RESPIRATION RATE OF SNAKES

The earliest study on the respiration of the cold-blooded animal is that reported by Paul Bert,<sup>1</sup> who gives a number of graphic tracings of the respiration of such cold-blooded animals as the tortoise, the boa, the lizard and the crocodile. The mechanism of the respiration of reptiles has also been extensively studied by Siefert<sup>2</sup> who includes, in the report of his observations, an admirable collection of literature with special reference to the investigations of Sibson<sup>3</sup> and Hofmann.<sup>4</sup> In his report Siefert records no respiration rates, since the chief emphasis was laid upon the mechanics of respiration. In the absence of definite information on the respiration rate of large serpents, action was taken in connection with our other studies, particularly the skin temperature measurements, to record the respiration rate of a few snakes. These records were obtained by observing the thoracic or abdominal movements and counting the time for ten complete respirations.

Four pythons were used in the first study in December 1916. Python 1 was the so-called "largest python," being a fine specimen approxi-

<sup>1</sup> Bert, P., *Leçons sur la physiologie comparée de la respiration*, Paris, 1870, p. 286.

<sup>2</sup> Siefert, E., *Arch. f. d. ges. Physiol.*, 1896, **64**, pp. 321-506.

<sup>3</sup> Sibson, F., *Philos. Trans.*, 1846, Pt. 4, p. 501.

<sup>4</sup> Hofmann, *Bronn's Klassen. u. Ordnungen d. Thierreiches*, Leipzig, 1890, **6**, Abt. IV, Reptilien. (Cited by Siefert.)

mately 7 meters long. Pythons 2 and 3 were approximately 5 meters long, and python 4 was a small Indian python. Three years later a boa constrictor and another large python were observed. This large python may possibly have been the same snake as python 1 observed in 1916, but no record was made as to its identity. The results of these observations are given in table 2. In each case the rate per minute has been computed from the count for ten minutes. Little difficulty was experienced in making the count, except that in the 1916 series pythons 1, 2 and

TABLE 2—*Respiration rate of snakes*

Snake and date since last fed	Date of observations	Time	Respiration rate per minute
	1916		
Python No. 1.....	Dec. 20	12 <sup>h</sup> 25 <sup>m</sup> p.m.	2.8
Dec. 19.		12 50	2.5
		2 36	3.0
Python No. 2.....	Dec. 20	12 33	1.3
Aug. 1.		12 43	1.3
		12 58	1.3
		2 25	2.1
		2 50	3.0
		2 56	2.8
Python No. 3.....	Dec. 20	12 19	2.2
Dec. 14.		12 37	2.0
		2 25	1.8
		2 36	2.2
Python No. 4.....	Dec. 20	3 00	3.4
Dec. 7.		3 10	2.7
	1919		
Python No. 1 (?)..	Nov. 6	.....	1.6
(7 meters)	Nov. 6	.....	1.6
	Nov. 8	.....	2.1
	Nov. 8	.....	3.0
	Nov. 10	.....	2.3
	Nov. 10	.....	2.3
	Nov. 7	.....	1.4
Boa.....	Nov. 7	.....	1.6
	Nov. 8	.....	2.1
	Nov. 8	.....	2.3
	Nov. 11	.....	1.7
	Nov. 11	.....	1.5

4 were at the time agitated as the result of previous handling for body-temperature observations, and hence the results are probably a little high rather than low. In the 1919 series the snakes were observed without removal from their den and had not been agitated. Frequently the first five respirations were counted and then the second five, and the time required in each case was noted. Thus, a check was obtained upon the counts, which practically always agreed well.

The temperature of the gravel in the cages in which the animals rested was in general in all the experiments not far from 30° C. In the 1916 series simultaneous or nearly simultaneous measurements of body tem-

perature, usually the temperature in the folds, occasionally the rectal temperature, were also secured to determine the probable temperature of the animal itself at the time these observations on respiration rate were made. Thus, on December 20, 1916, when the first records of respiration rate were made, the temperature of python 1 between the folds averaged approximately 29° C. and that of pythons 2 and 4 between the folds about 30° C. (See table 5, page 58.)

Under the moderately high environmental temperature, the respiration rate of python 1 on December 20, 1916, averaged 2.8 per minute. The python had eaten a pig at 6 p.m. the night before, that is, 18 hours before. This of itself is ample reason to explain the high respiration rate noted with this snake. In November 1919, when presumably python 1 was observed again, the respiration rate on the first day was approximately half that noted in December 1916. There is no record of when this large python was last fed previous to November 6, 1919, but judging from the comparison of the results obtained in 1916 and 1919, we believe that digestion as such undoubtedly plays an important rôle in the respiratory activity of even these cold-blooded animals. The discussion given later (see pages 247 to 328) regarding the metabolism of these snakes during digestion will show the need for a change in respiration rate to provide for the removal of the carbon dioxide produced incidental to digestive activity. On November 8 and 10, 1919, the respiration rate of python 1 was somewhat more rapid. The second count on November 8, a rate of 3 respirations per minute, was obtained a few moments after the snake had made some movement.

Two medium-sized pythons, Nos. 2 and 3, were studied on December 20, 1916, in separate chambers. Python 2 had been fasting since August 1. The first three observations with this python showed a rate of about 1.3 per minute. The subsequent rates were much higher and are to be explained by the fact that between the third and the fourth readings the snake had been taken out of the chamber and the rectal temperature (29° C.) recorded. The python was much agitated as a result, and hence a persistently high respiration rate was maintained during the rest of the period of observation.

Python 3 had a respiration rate somewhat higher than the first three records for python 2. The latter had been fasting since August 1, whereas python 3 had been fed only six days before the respirations were counted, and undoubtedly there was an increased metabolism and increased respiratory activity following the digestion of food. However, python 3 was not subjected to any handling for body-temperature measurements on December 20 and its respiration rate was distinctly lower than the last three records for python 2, which had been fasting for several months but had been agitated by being taken out of its cage for body-temperature measurements.

Python 4 had been fasting for 14 days, but was much agitated. It had been placed in a box by itself on December 18, and was distinctly restless

at 1<sup>h</sup> 50<sup>m</sup> p.m. on December 19. At 3<sup>h</sup> 30<sup>m</sup> p.m., December 20, it was still too agitated to handle to take the rectal temperature. This therefore accounts in part for the higher respiration rate found with this snake.

The boa observed on November 7 to 11, 1919, had been in a respiration chamber for some time before. Rectal temperatures of this particular snake were not taken. The boa weighed approximately 4.5 kg. The respiration rate on the three days varied from 1.4 to 2.3, being definitely higher on November 8 than on November 7 and 11.

The respiration rate of all these snakes is strikingly low, averaging 2.1 respirations per minute. The well-known retarded respiration rate of hibernating warm-blooded animals and of dormant cold-blooded animals can not be used for comparison here, because probably most of these snakes had a rectal temperature of not far from 30° C. and hence, as will be seen later, had a fairly active metabolism. The rates are extraordinarily low, probably the lowest in the animal kingdom, although there is the unique instance of a human, a young woman, who has a respiration rate of 3 per minute.<sup>1</sup> With these snakes it was difficult to secure any information with regard to the volume of respiration and the regularity in depth of respiration, and we can simply record these low rates as characteristic of these large cold-blooded animals, when at a body temperature of probably not far from 30° C. Groebbels<sup>2</sup> maintains that with warm-blooded animals there is a close relationship between the oxygen consumption and the respiration rate and that both the respiration rate and the oxygen consumption decrease as the environmental temperature becomes lower. Undoubtedly our snakes would have shown an even lower respiration rate had the body temperature been much lower,<sup>3</sup> but the cost of these large serpents and the danger of exposing them to low temperatures made any special tests at a low temperature impracticable.

The respiration rate of an incubating python was likewise studied by us. The discussion of these records will be found on pages 97 to 101 and the records themselves are tabulated in tables 16 and 17, pages 99 and 100.

## BODY TEMPERATURE OF SNAKES

### COMPARISON OF MOUTH AND RECTAL TEMPERATURES

With warm-blooded animals when one speaks of body temperature, one may mean the temperature taken in any of the several cavities of the body. With humans the body temperature is frequently taken in the mouth or even in the axilla but, physiologically, human temperatures are those taken either in the vagina or the rectum, that is, in a deep cavity. It is well known that among humans and other warm-blooded animals the temperature in the rectum, the ideal body cavity for temperature measurements, is considerably higher than that of the extremities. The snake

<sup>1</sup>Benedict, F. G., *Bull. Soc. Sci. d'Hygiène Alimen.*, 1929, **17**, p. 321.

<sup>2</sup>Groebbels, F., *Arch. f. d. ges. Physiol.*, 1925, **208**, p. 661.

<sup>3</sup>Britton (*Amer. Journ. Physiol.*, 1924, **67**, p. 418) finds that the respiration rate of fish varies with the temperature of the surrounding medium.

may be considered as an elongated cylinder with no appendages. What is the distribution of temperature in this animal? The snake rarely lies stretched out, but almost invariably is coiled upon itself in folds. In experimental work with this animal, part of the snake's body may be exposed to the room air, part may be resting on a metallic box, on sand or against wood, and as a result of the folds, the thickness of tissue material becomes greatly enlarged. What is the temperature at different parts of the snake's body? Fortunately we have with the snake two deep cavities, in the mouth or throat and in the cloaca. Our study of the snake's body temperature, therefore, will deal first with a comparison of the temperatures of the mouth and the rectum.<sup>1</sup> It would be logical and desirable, perhaps, to extend the comparison to study simultaneously the skin temperature at various parts along the length of the body, but since the snake is seldom stretched out, our first study deals only with the comparison of the temperatures of the mouth and the rectum. In the snake the distance between these two cavities is relatively great when compared with the size of the animal itself. With warm-blooded animals one argues usually that the heat production and the rapid circulation of the warm blood produce an equalization of temperature throughout the body. This is not true, as pointed out above, for the temperature of the extremities is considerably lower than that of the trunk. With the snake almost nothing is known regarding the circulation of the blood or even the heart rate. The only records of the heart rate of snakes that we have been able to find are those reported by Wilford<sup>2</sup> in 1819, who studied a boa constrictor in Africa at an environmental temperature of about 25° C. and found on five occasions a heart rate varying from 15 to 25 beats per minute, the majority being nearer 24 or 25.

In our study a comparison of mouth and rectal temperatures was not the major feature. Incidentally on a few occasions such measurements were actually made, and the results are incorporated in table 3. The first comparison was made on December 20, 1916, with a python (No. 2) approximately 5 meters long. The serpent had been taken from its cage by five men, and the first rectal-temperature record was obtained in less than three minutes after the snake was first seized. The time between the first and second readings of rectal temperature, which were, respectively, 29.0° and 28.9° C., was about 5 minutes. The mouth temperature taken at the same time was 29.2° C. That the snake had been exposed for approximately 7 minutes to a room temperature of 22.2° C. with no greater effect upon the temperature than is noted here is interesting. A second series of observations was made with the same snake in 1917. After the first reading at 3 p.m. on January 17, the snake was put in a large respiration chamber in the reptile house and remained there overnight and during the next day. The rectal temperature was 25.9° both

<sup>1</sup> Except in those sections where it is definitely stated that the body temperatures were taken during digestion, all the body temperatures were taken, so far as we know, when the snakes were in the fasting condition.

<sup>2</sup> Wilford, Journ. Sci. and Arts, Roy. Inst. Great Britain, London, 1819, 6, p. 115.

at 3 p.m. and at 4<sup>h</sup> 20<sup>m</sup> p.m. The mouth temperature was 25.3° and 26.1°, respectively. The other observations which follow, two on January 18 and two on March 2, show at one time a temperature in the mouth a little below that in the rectum and at another time a temperature in the mouth a little higher. Practically there is no difference between the two.

On March 2 the snake was taken from the cage at 11<sup>h</sup> 19<sup>m</sup> a.m. and the temperatures were noted. The snake was then carried by five men outdoors from the reptile house to the primate house at the Zoological Park, arriving there at 11<sup>h</sup> 31<sup>m</sup> a.m., thus being exposed to the outside temperature of 0.5° C. for 10 minutes. As a result of this exposure the temperature in the rectum fell 2.6° and that in the mouth 2.0° C. In spite

TABLE 3—*Comparison of mouth and rectal temperatures of a python*

Date	Time	Body temperature	
		Rectal	Mouth
Dec. 20, 1916	1 <sup>h</sup> 45 <sup>m</sup> p.m. 1 50	°C. 29.0	°C. 29.2
		28.9	....
Jan. 17, 1917	3 00	25.9	25.3
Jan. 17, 1917	4 20	25.9	26.1
Jan. 18, 1917	11 05 a.m.	23.8	23.7
Jan. 18, 1917	4 30 p.m.	21.9	22.6
Mar. 2, 1917	11 19 a.m.	26.9	26.4
Mar. 2, 1917	11 31	24.3	24.4

of the sudden change in environmental temperature therefore, the mouth and rectal temperatures, which were essentially the same before the exposure, were practically identical after the exposure. It is obvious that the sudden removal by five men of a large snake from its environment in the snake den subjects the animal to a considerable amount of exercise that is certainly in the nature of an insult and may perhaps be the cause for a rise in body temperature. It is also obvious that the mere handling of the snake by the warm-blooded human hands may result in raising the snake's body temperature (see pages 59 to 61). Hence it is surprising that in this experiment of March 2, 1917, the temperatures were so nearly the same in the mouth and the rectum.

Apparently whatever may be the extraneous factors affecting the body temperature of snakes (even such factors as marked change in environmental temperature, handling and agitation), the temperatures in the rectum and in the mouth are practically the same. It is perhaps surprising that the temperature is so uniform in the mouth and the rectum, for the respiratory act in a snake must of necessity involve inhaling air, usually not saturated, and then exhaling air probably saturated at the temperature of the animal. In so doing there must be a local cooling



effect of the trachea. This, one would imagine, might lower the mouth temperature. Little is known regarding the heart rate of snakes, but one can conceive that the circulation of the blood might be so sluggish that the local cooling of the trachea would have an imperceptible effect upon the rectal temperature.

#### COMPARISON OF SKIN AND RECTAL TEMPERATURES

With warm-blooded animals it is well known that the skin temperature is invariably somewhat lower than the internal, rectal temperature, at times much lower, depending in large part upon the extremities and the circulation of the blood, particularly the surface or cutaneous circulation. With cold-blooded animals, where the difference normally between the temperature of the environment and the temperature of the animal is much less than it is under ordinary conditions with warm-blooded animals, the question arises as to how the skin temperature compares with the temperature of the internal part of the body, either the mouth or the rectum. The skin temperature of any animal is the resultant of several factors. With warm-blooded animals there is a normal loss of heat through the skin by radiation, there is the cooling effect of vaporization of water from the skin, and with mammals there may frequently be an actual excretion of water through the sweat glands. If the warm-blooded animal or human comes into an environment warmer than itself, it is possible that the skin temperature may be increased by the absorption of heat from the environment. With cold-blooded animals, particularly snakes, the situation is much different. A *very small* amount of heat is produced and, as is well known, the body temperature is not far from that of the environment. Hence there would be little, if any, loss of heat through the skin by radiation. There is, however, the cooling effect of the vaporization of water, not only from the skin but likewise from the lungs, and because of the diurnal changes in environmental temperature and sunning to which many animals are subjected, there may be a time when the animal is actually warmed by absorbing heat from the environment itself. Under these conditions it is conceivable that the internal temperature of the animal would be colder than the external, for as the animal is warmed it would absorb heat from the environment and the skin would be nearest the source of heat.

The cooling effect of the vaporization of water upon the body temperature of humans has already been noted. Air, which enters the lungs of a man approximately 60 per cent saturated at ordinary room temperature, for example, and comes out saturated at 34° C. or thereabouts, brings with it the latent heat of water vapor. This vaporization of water has so cooled the tissues inside that they may conceivably be cooler than the body surface. Our comparison of the mouth and rectal temperatures of a python indicates that with snakes the temperature of the rectum is essentially that of the mouth, that is, the local cooling effect in the mouth is practically negligible, for no similar cooling effect could be ascribed to the

section of the animal near the rectum. According to Wilford,<sup>1</sup> the boa constrictor has a heart rate of not far from 15 to 25 beats per minute at about 25° C. This is a slow rate when compared with that of the albino rat, but not lower than that noted with steers during undernutrition<sup>2</sup> and therefore not outside the range found in experimentation with warm-blooded animals. But it is conceivable that such circulation of the blood would materially aid in equalizing, in part at least, the temperature distribution throughout the entire body and thus compensate for any localized heating or cooling effect. It is therefore obvious that a study of the skin temperature itself, and particularly as compared with the internal temperature (mouth or rectum), is an important physiological problem dealing with the total heat loss and the path of heat loss in snakes.

Although our research included a large number of rectal-temperature records, the actual number made at *the same time* that the skin temperature was recorded is small. Our first comparison of skin and rectal temperatures was made with python 2 in New York on December 20, 1916. The animal had been lying in a cage for some time, and the temperature in the folds of the snake, determined by means of a thermo-junction (see fig. 16, page 44), averaged not far from 31° C. The temperature of the air in the cage, about 30 cm. above the graveled floor, averaged 25° C. It is certain, however, from other experiments that the true gravel temperature was much higher. With a small python in a subsequent series of observations on rectal temperature alone, the temperature of the gravel was found to be 27.3° C., a point 10 cm. above the gravel was 25.0° C., and a point 30 cm. above the gravel was 23.4° C., or 4° lower than the gravel temperature. We have reason to believe, therefore, that in the experiment with python 2 on December 20 the gravel temperature must have been at least four or five degrees warmer than that 30 cm. above the floor, or not far from 30° C. After the skin temperature measurements, the python was taken from the cage by five men, to be transferred to an adjoining room containing the respiration chamber. This operation required about 3 minutes. The thermometer was then placed in the rectum and the body temperature recorded. The temperature of the room in which this measurement was taken was 22.2° C. The rectal temperature was 29.0° C. and the mouth temperature, taken at essentially the same time, 29.2° C. A second rectal-temperature measurement was made about 5 minutes later, and in that time the temperature had fallen only 0.1° C. This first comparison would suggest that the rectal temperature of the snake is slightly *lower* than the skin temperature. The skin temperature was measured by the usual thermo-electric junction and the rectal temperature by a mercurial thermometer. Python 2 became restless after it was put back in the cage, moved around a good deal, and finally drank some water. Further observations were therefore precluded.

<sup>1</sup> Wilford, *loc. cit.*

<sup>2</sup> Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 193.

In February 1920, a 3-meter boa (boa N) was brought from the New York Zoological Park to Boston and studied at the Nutrition Laboratory with special reference to skin and rectal temperatures. The results of this study are reported in table 4. On the night of February 27 the boa was placed in a box and put inside a respiration calorimeter with free ventilation. The calorimeter was heated so that the average environmental temperature throughout the night was about 30° C. At 8<sup>h</sup>49<sup>m</sup> a.m., February 28, the boa was taken from the calorimeter, removed from its box, and six records of rectal temperature were obtained at 15-second intervals. These successive readings and others made on subsequent days showed that about 45 seconds were required for the mercurial thermometer

TABLE 4—Comparison of skin and rectal temperatures of boa N

Date	Time	Skin temperature							Rectal temperature
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>f</i>	Average	
1920		°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.
Feb. 28	8 <sup>h</sup> 49 <sup>m</sup> a.m.	.....	.....	.....	.....	.....	.....	.....	28.30
	1 06 p.m.	28.60	28.60	28.74	29.34	29.62	28.56	28.91	29.55
	4 30	25.21	25.78	27.00	27.61	28.88	27.08	26.93	.....
	4 35	26.43	26.47	28.22	27.82	28.39	27.90	27.54	27.17
Mar. 1	9 00 a.m.	15.26	15.26	15.63	15.95	16.28	15.67	15.68	15.53
	4 26 p.m.	14.35	14.42	14.89	15.00	15.31	14.89	14.81	15.07
Mar. 2	9 00 a.m.	14.42	14.38	14.65	14.77	14.64	14.47	14.56	14.02
Mar. 3	12 15 p.m.	21.27	21.49	21.51	22.07	22.46	21.65	21.74	22.57
	4 03	22.99	23.12	22.75	23.49	.....	.....	23.09	23.56
Mar. 4	11 01 a.m.	25.72	25.92	26.04	26.97	27.97	.....	26.52	28.55
	4 07 p.m.	24.33	24.50	25.25	25.13	25.40	26.00	25.10	25.42

to register a constant temperature after being inserted in the rectum. The values for rectal temperature given in table 4 are therefore *average* values, based upon a series of records in each case continued until the thermometer gave constant readings. After the rectal-temperature records at 8<sup>h</sup>49<sup>m</sup> a.m., boa N was put back into the calorimeter. At 1<sup>h</sup>06<sup>m</sup> p.m. it was removed and a series of six skin-temperature measurements was made as the snake lay coiled in the small metallic box. This was followed by a series of rectal-temperature measurements. The points on the snake's body at which the skin temperature was observed have been indicated by the letters *a* to *f* in table 4. All of the measurements at positions *a* and *b*, the last four at position *c*, the last one at position *d*, and all but the last at position *f* were on the top, exposed parts of the snake. The first five measurements at position *c*, all but the last at position *d* and all at position *e* were made between the coils or between the coils and the box. At 4<sup>h</sup>07<sup>m</sup> p.m. on March 4 position *f* was on the belly at the bottom of the box. The entire series of skin-temperature measurements required about 2 minutes in each instance, and rectal-temperature measurements immediately followed each series.

On February 28 at 1<sup>h</sup>06<sup>m</sup> p.m. the skin temperature at position *e* was a little above the average rectal temperature, but was definitely below it at all the other points. At 4<sup>h</sup>35<sup>m</sup> p.m. four points were above and two below the internal body temperature. The boa was then placed in the calorimeter overnight at a much lower environmental temperature (15.5° C.). At 9 a.m., March 1, four points on the skin were above and two below the rectal temperature; at 4<sup>h</sup>26<sup>m</sup> p.m. only one point was above. Practically all of the skin temperatures that were higher than the rectal temperature were, however, taken between the coils and not on the exposed surface, indicating that vaporization of water was retarded by the coiling of the snake.

After another night spent in a cool environment, boa N was measured again on March 2, at 9 a.m. The skin temperature was in every instance higher than the rectal temperature, but the conditions of measurement were undoubtedly abnormal in this series for at 9<sup>h</sup>02<sup>m</sup> a.m., when the boa was taken out of the box to be weighed, considerable moisture was found condensed on its body and there was moisture in the box. The animal was given water to drink and left all night in an environment at about 26° C. On March 3 at 12<sup>h</sup>15<sup>m</sup> p.m. and again at 4<sup>h</sup>03<sup>m</sup> p.m. the skin temperature was in every instance lower than the rectal temperature. After the snake had spent another night at a higher temperature (31° to 32° C.) its rectal temperature at 11<sup>h</sup>01<sup>m</sup> a.m., March 4, was materially higher than that at any point on the skin. By design the environmental temperature was lowered about 2° C. at 12 noon. This accounts for the lower body temperatures at 4<sup>h</sup>07<sup>m</sup> p.m. The skin at position *f* was warmer than the rectal temperature, probably explained by the fact that position *f* in this instance was on the belly of the snake near the bottom of the box.

If we rule out those observations made between the coils and at points on the body where radiation was hindered, exclude the abnormal series on March 2, and consider only the temperatures of those surfaces not touching the metal walls of the box or protected by the coils of the snake itself, we find that in all but two cases the surface temperature was somewhat lower than the rectal temperature.

#### COMPARISON OF SKIN AND ENVIRONMENTAL TEMPERATURES

Our first observation on the skin temperature of snakes was an attempt to note whether there is any differential between the temperature of the skin and that of the environment. Obviously for this purpose the thermo-junction suggested itself as the ideal method. A copper-constantan junction was constructed and calibrated and the usual adjustment with galvanometer and resistance boxes arranged, so that any degree of sensitivity of the galvanometer could be obtained. Since we knew that in all probability we would be dealing with small temperature differences, perhaps of two- or six-tenths of a degree, the adjustments were made so that the galvanometer showed a deflection of approximately 27 mm. per degree. The sensitivity of the junctions and the number of millimeters

per degree deflection of the galvanometer were determined by calibration, by immersing the two junctions in two Dewar flasks with a temperature difference of approximately 5 degrees. The two junctions were tied to a light bamboo pole, the tip of a fishing rod. To this pole was lashed likewise a mercurial thermometer with easily readable scale, in such a position that one thermo-junction could actually be entered between the folds of the snake and the other thermo-junction would be in the air above it but in direct contact with the bulb of the mercurial thermometer.

TABLE 5—*Skin temperature of snakes*

Snake and date	Time	Temperature in folds of snake	Temperature on pole near snake
		°C.	°C.
1916 Python No. 1 Dec. 19	1 <sup>h</sup> 50 <sup>m</sup> p.m.	27.59	24.95
	2 03	28.04	24.65
	2 05	28.06	25.05
	2 07	29.44	26.35
Dec. 20	11 50 a.m.	29.83	25.65
	11 56	29.40	25.55
	1 40 p.m.	29.38	25.05
		30.51	25.85
	3 22	29.46	24.95
	3 27	30.76	25.55
Python No. 2 Dec. 19	1 58	31.33	26.05
	2 12	30.02	25.15
Dec. 20	11 45 a.m.	30.68	24.95
	12 03 p.m.	31.62	25.75
	1 32	30.82	24.95
	3 33	30.10	25.55
Python No. 4 Dec. 19	1 50	28.93	24.95
	2 05	29.45	24.95
	2 10	30.55	26.05
Dec. 20	11 54 a.m.	31.12	25.95
	12 00 noon	30.35	25.95
	1 37 p.m.	29.90	25.35

Our comparisons of the skin and the environmental temperature were made with pythons 1, 2 and 4 on December 19 and 20, 1916 (see table 5). Python 1 had eaten at 6 p.m., December 19. Python 4 had been placed in a box by itself on the afternoon of December 18. This resulted in considerable agitation. It was assumed it would settle down during the night, but the snake was still restless when observed at 1<sup>h</sup>50<sup>m</sup> p.m., December 19. When the snake was touched with the bamboo pole, there was a reflex action which resulted in the snake drawing away from the point of contact.<sup>1</sup> The junction could then be inserted in a fold and the

<sup>1</sup>This reaction noted with all the snakes with which we worked is in striking contrast with the report of FitzSimons (*Pythons and their Ways*, London, 1930, pp. 29 *et seq.*) who records many instances where rats had eaten pythons, had sucked sufficient blood to kill the snake, and often had eaten a number of pieces of flesh along the backbone of the snake. FitzSimons suggests that the python is insensible to pain in this way.

snake usually settled down again, so that there was a real contact between the fold and the junction. In this way several observations were made. The mercurial thermometer was read through the glass front of the snake cage by means of opera glasses. This so attracted the attention of the snakes themselves that there was no difficulty in inserting the pole through the door of the snake den at the front end of the cage and manipulating the wires leading to the galvanometer. The galvanometer indicated the difference in temperature between the mercurial thermometer on the pole near the snake and the junction in the fold of the snake, and with this mercurial thermometer as a standard or constant junction the temperature of the folds of the snake could be computed. But the difficulty of this procedure was that, although it showed a difference of about 5 degrees between the temperature of the air and that in the fold of the snake, we found later that the temperature of the air at this level was measurably lower than that of the real environment of the snake. Actually in these tests the snake rested on a gravel bed, well heated by steam coils beneath, and there was a pronounced gradient in temperature as the distance above the gravel bed increased. In one instance (see page 55) the temperature of the gravel was 4 degrees higher than that of the air 30 cm. above the gravel, which was the position usually occupied by our thermometer in these particular tests. Since we have no definite assurance as to what the temperature of the environment was in these particular experiments, we can make no comparison of the skin and the environmental temperatures. These observations are therefore of chief importance in accentuating the difficulty of comparing the skin temperature with the environmental temperature and in bringing out clearly that the temperature of the environment is frequently far more in question than that of the skin itself. It is precisely this type of observation that challenged the reported findings of body temperatures much above the environment in the case of the incubating python. (See pages 86 to 114 for further discussion of this point.)

#### FACTORS AFFECTING RECTAL TEMPERATURE OF SNAKES

##### HANDLING AND RECTAL TEMPERATURE

As hinted on page 53, it was noted in the course of our various measurements that the mere handling of snakes by the warm human hand (the temperature of which is normally not far from 30° C.<sup>1</sup>) may result in raising the snake's body temperature. The snake is usually grasped just back of the head, especially when mouth temperatures are taken, and the local area may be warmed by the hands of the operator. This problem of local warming of the snake by the hands of humans has given us much trouble, for it was our frequent experience that the snake coiled itself about the warm parts of the human body such as the neck, the wrists, and the arms, at times seemingly for the benefit of the heat. The literature

<sup>1</sup> Benedict, F. G., Asher-Spiro's *Ergebnisse der Physiologie*, 1925, **24**, p. 594.

is full of confusing statements regarding the body temperature of snakes, and several investigators, notably Berthold,<sup>1</sup> have expressly mentioned the difficulty of determining the true temperature of cold-blooded animals. Wilford<sup>2</sup> was perhaps the first to point out that handling might increase the body temperature. He reports many instances where the rectal temperature of the snake was a little below that of the environment, although in the majority of cases it was at or above the environmental temperature. We therefore planned specifically to study the effect upon the rectal temperature of the snake of contact with the human hands of the observer. Two tractable, placid gopher snakes were selected for this study which, because of their small body weight, would absorb heat from the operator more rapidly than would a larger snake. Each snake was placed in a chamber of constant temperature and left there for a sufficiently long period until its body temperature was essentially that of the environment. The snake was then taken out of the chamber, the thermometer was inserted in the rectum, and the body temperature read every minute. In a typical instance the snake showed a rectal temperature of 17.55° C., one minute after removal from the chamber. There was then a constant increase from minute to minute until the sixth minute, the successive readings being 17.71°, 17.81°, 17.98°, 18.24°, and 18.53° C. In the seventh, eighth, and ninth minutes there was a rapid increase in temperature, the records being 19.88°, 20.85°, and 20.95°, respectively. This increase is explained by the fact that during these three minutes the snake was moving somewhat. From the tenth to the thirteenth minutes the body temperature continued to rise slowly to a value at the thirteenth minute of 21.81° C.

Roughly speaking, with a snake of this type the rectal temperature will increase about one-tenth of a degree each minute when the snake is taken from a constant environmental temperature and brought into contact with warm human hands. That this increase is not due to agitation was clearly shown whenever the snake moved, for in those cases (as illustrated above) the increase was usually somewhat greater. As the outcome of 24 series of observations of precisely this character on two gopher snakes we are convinced that at environmental temperatures of 23° C. and below a considerable amount of heat is absorbed by the snake from the body of the operator. Experiments were not carried out at higher environmental temperatures to study the effect of handling, but these observations with gopher snakes illustrate clearly the difficulty of securing true body temperatures, either rectal or mouth, of snakes when they must be handled. The heat given up to the snake by the body or the skin of the operator is a factor that must always be taken into consideration. This heat makes for an increase in the snake's body temperature, so that the true rectal temperature is probably somewhat lower than what is recorded on the thermometer. We believe that our experiments show that this heat absorption is entirely independent of any agitation of the snake, for with

<sup>1</sup> Berthold, A. A., *Neue Versuche über die Temperatur der kaltblütigen Tiere*, Göttingen, 1835.

<sup>2</sup> Wilford, *Journ. Sci. and Arts, Roy. Inst. Great Britain, London*, 1819, **6**, p. 115.

agitation and movement our thermometer always showed a greater rise in body temperature than when the snake was resting quietly, as was usually the case.

#### AGITATION AND RECTAL TEMPERATURE

In several of our experiments in taking rectal temperatures it was noted that, when the snake moved or seemed to be unduly agitated, the rectal temperature rose. This was entirely independent of any absorption of heat from the body of the operator. To study the effect of agitation alone we made a series of experiments with boas I and D, the results of which are reported in table 6. In these experiments the snake rested overnight in a box in the laboratory, usually without any special heating device so that the temperature of the box was essentially that of the laboratory itself. In each experiment the snake was taken out of the box before the rectal temperatures were recorded, into a room at about 23° C., and was deliberately agitated between the different readings. The rectal temperature increased markedly in all cases as a result of the agitation. Although these experiments were made in July, these rises in rectal temperature are not due to the fact that the temperature of the room was unduly high, as might be expected from midsummer weather. Indeed, at the end of each series the temperature of the snake was usually considerably above the room temperature so that the room temperature could not have played any great rôle. Likewise the heat taken from the operator's hands, although undoubtedly contributing somewhat to the increased body temperature of the snake, could not have been entirely responsible for the striking increases in rectal temperature.

In the last experiment reported in table 6 boa D had spent considerable time previously at a fairly high environmental temperature, approximately 28° C. Under these conditions, when the rectal temperature was taken and the snake agitated at a room temperature of about 23° C., the agitation had little effect upon the rectal temperature. In other words, the snake started with a high body temperature, and the agitation had little direct effect upon the rectal temperature. Since the environmental temperature was now 5 degrees below the previous environmental temperature, one would have expected a fall in the snake's temperature. The agitation actually prevented the normally expected fall.

These experiments demonstrate that the agitation, excitation, or active movement of the snake results in an internal heat production that increases the rectal temperature appreciably above the temperature of the environment. The effect of agitation in raising the rectal temperature of reptiles has also been noted by Sutherland,<sup>1</sup> who found that the great blue-tongued lizard could increase its body temperature as much as 0.5° in 10 minutes of anger. The significance of the reaction of rectal temperature to agitation in relation to metabolism will be considered in a later chapter of this report, in the discussion of the metabolism as affected by agitation. (See page 152.)

<sup>1</sup> Sutherland, A., Proc. Roy. Soc. Victoria, 1897, N. S., 9; *ibid.*, Nature, 1897-98, 57, p. 67.



The snake loses heat by reason of the temperature potential between its surface and the environment. If the loss of heat by this potential is not equivalent to the production of heat, the snake's temperature will definitely rise. The heat-regulating mechanism of the snake is so poor that there is practically no surface circulation. Hence even with a moderate amount of activity there will be a rise in body temperature, if the animal can not lose heat fast enough. From the teleological standpoint, this is of distinct advantage to the snake. For example, as its body temperature rises the snake becomes more active, and its protoplasm is more receptive to stimuli, either for purposes of attack or to avoid danger from other animals. The interesting problem arises as to whether it would

TABLE 6—*Effect of agitation on rectal temperature of snake*  
(Room temperature 23° C.)

Snake <sup>1</sup> and date	Time	Rectal temperature	Snake <sup>1</sup> and date	Time	Rectal temperature
		°C.			°C.
1917	10 <sup>h</sup> 50 <sup>m</sup> a.m.	22.7	July 5	11 <sup>h</sup> 06 <sup>m</sup>	20.9
Boa I:	11 00	23.9		11 10	21.6
July 3	11 05	25.4		11 15	22.2
	11 15	27.1		11 20	23.0
	11 25	28.9		11 25	23.8
July 4	11 01	21.7	July 6	11 36	20.8
	11 05	22.7		11 40	21.1
	11 10	23.3		11 45	22.1
	11 15	24.1		11 50	22.9
	11 20	24.6		11 55	23.7
			Boa D:		
			July 6	4 00 p.m.	28.0
				4 05	28.2
				4 10	28.1

<sup>1</sup> Agitated between measurements.

be possible to produce in the snake a self-induced rise in body temperature to such a point that there would be something in the nature of a heat stroke. Or as the body temperature rises, would the reaction to stimuli be such that the animal would be simply exhausted by the higher temperature and would fail to fight or engage in muscular activity to produce sufficient heat to raise the temperature above any danger point?

#### RECTAL TEMPERATURE WITH UNCHANGING TEMPERATURE OF ENVIRONMENT

Our observations of rectal temperature were made primarily to study the relationship between the rectal temperature of the snake and the temperature of the environment. As we have already seen, the difficulty of obtaining true rectal temperatures is great. The very act of handling these serpents may result in muscular activity on the part of the animal, with increased heat production and increased body temperature incidental thereto. The snake is likewise affected by the heat from the hands or body of the operator handling it, and offsetting this is the cooling effect of the room air, for often the snake was taken out of a somewhat warmer

temperature than that of the room in which the observations were made. A careful study of the relationship between the rectal temperature of the snake and the temperature of the environment was therefore made in the Nutrition Laboratory under conditions where the snake had been for a long time at a constant room temperature and was measured at this constant temperature, with the effects of handling and agitation completely ruled out.

In our comparison of the skin and rectal temperatures of the snake (see p. 56), we found that the coiling of the snake upon itself inside the metal box made for an uneven, perhaps irregular heat loss with possibility for divergence of observations, depending upon what part of the snake was measured.<sup>1</sup> Believing that if the snake could be prevented from coiling, the conditions for heat loss would be much more uniform, a snake (boa N) was placed in a straight, wire-mesh tube made of metallic mosquito-screening. This tube was closed at the head end and was long enough and narrow enough so that the snake could not coil upon itself. Thus the entire surface of the body was exposed to the air. The tube was then suspended inside a 20-cm. pipe, longer than the tube itself, and the snake was allowed to remain in the laboratory in this tube overnight. A stream of air was driven through the 20-cm. pipe by a blower. In the morning two mercurial thermometers near the head and the tail of the boa registered 18.60° C., and from there on for three hours an assistant carefully regulated the environmental temperature to hold the two thermometers as nearly as possible at 18.6° C. The fluctuations did not amount to over  $\pm 0.2^\circ$  C.

The thermo-junction system (see page 43) was used for measuring the rectal temperatures. The two junctions, when placed in the air current, showed *no deflection* on the galvanometer. A further check on the sensitivity and accuracy of the galvanometer was obtained by dipping the junctions in two Dewar flasks containing alcohol, with a temperature difference of about 2 degrees. Two calibrations under these conditions indicated that each millimeter deflection of the galvanometer was equivalent to 0.0133° C. One junction was placed near the thermometer that was in the tube near the tail of the boa. The other junction was placed through an opening in the center of an aluminum tube inserted in the cloaca of the snake. With the junctions thus located, a series of measurements at 12 noon showed that the average temperature of the mercurial thermometers in the air current at the head and the tail of the snake was 18.62° C. and that, according to the galvanometer deflections, the rectal temperature was 16.74° C. or nearly 2 degrees *lower* than the environmental temperature. The galvanometer zero was then tested again, and another series of observations at 12<sup>h</sup>17<sup>m</sup> p.m. gave thermometer readings of air temperature averaging 18.63°, with a galvanometer deflection indicating a rectal temperature approximately 2 degrees lower. From this second series of observations it seemed as if the temperature of the snake was slowly rising, so the snake was left in the tube for another hour and at

<sup>1</sup> A most critical experimental handling of this type of problem with humans has just been published by H. Bohnenkamp (Arch. f. d. ges. Physiol., 1931, **228**, pp. 40-168).

1<sup>h</sup>31<sup>m</sup> p.m. measurements were made again. The air temperature at this time, being carefully controlled, remained at 18.62° C. The galvanometer now showed a deflection corresponding to a difference in rectal temperature noticeably greater than that in the preceding hour. Throughout the entire time the measurements were made in a rapidly moving current of air, which removed water from the animal's body by vaporization. Consequently the boa was always actually colder than the environment.

In the next test the ventilation was stopped and the animal allowed to remain in still air at a temperature as near 18° C. as possible, by controlling the temperature of the room. Under these conditions one would expect that the boa's body temperature might rise somewhat. At 2<sup>h</sup>37<sup>m</sup> p.m., when the snake had been an hour in still air, the blower was started again, and a moment or two later another series of readings was taken. These measurements showed that there was a slight, though probably insignificant rise in rectal temperature from 16.46° C. at 1<sup>h</sup>32<sup>m</sup> p.m., to 16.57° C. at 2<sup>h</sup>37<sup>m</sup> p.m. Two different mercurial thermometers were then inserted in the rectum and gave readings of 16.78° and 16.88° C., respectively. But the handling of the animal with the warm hands would tend to make for a slightly higher temperature with the mercurial thermometer.

All these experiments point conclusively to the fact that in a constant environmental temperature, without handling or agitation, the snake had a rectal temperature *below* the room temperature, that is, from 1.5° to 2° below. The vaporization of water from the skin of the animal undoubtedly contributed to this lower rectal temperature. The snake may therefore be compared to a wet bulb thermometer, for just as the temperature of a thermometer is lowered by vaporization of the water on the surface of the wet bulb, so is the internal temperature of the snake lowered by vaporization of water from the skin and consequent loss of heat. If the snake is studied in other than saturated air, much vaporization of water from its body is possible, and theoretically the real rectal temperature would then be much below the environmental temperature. We did not find pronounced differences between the temperature of the rectum and that of the environment, although our observations were usually made in relatively dry air, at least not in saturated air. But because of the influence of humidity, it is believed to be wise, whenever feasible, to record the rectal temperature of the cold-blooded animal in connection with any metabolism observations.

Numerous observers have noted the effect of changes in the temperature and the humidity of the air upon the rectal temperature of cold-blooded animals. The extreme conditions imposed by John Hunter,<sup>1</sup> who placed his snake in an atmosphere of 108° F. (42° C.), are, to be sure, rare. The animal was allowed to stay only 7 minutes in this temperature, when the temperature in its stomach and anus was found to be 99.5° F. (37.5° C.). The temperature could not be raised above this point in the

<sup>1</sup> Works of John Hunter (Palmer Edition), London, 1837, 4, p. 148.

atmosphere employed, undoubtedly due to the rapid vaporization of water. Soetbeer<sup>1</sup> has made a most extensive survey of the literature on the body temperature of poikilotherms,<sup>2</sup> and likewise made observations himself on the crocodile and the alligator. He concludes that when the animals were in saturated air their temperature was above that of the environment, but when they were in dry air their temperature was much lower than that of the environment. Soetbeer's article is especially to be recommended on account of the admirable treatment of the early literature on the body temperature of cold-blooded animals. Hall and Root,<sup>3</sup> using a thermo-electric method for determining the temperature in the rectum of various animals, noted that the rectal temperature was frequently much lower than the environmental temperature and that with amphibia in very dry air the rectal temperature was as much as 8 or 9 degrees lower. In air 95 to 100 per cent saturated, the rectal temperatures were less than 1 degree lower. The rectal temperature of reptiles was considerably less affected by the humidity, but always in the same manner, that is, in very dry air the rectal temperature was somewhat below the environment and in saturated air it was generally somewhat above. Hall and Root point out that the lower in the phylogenetic series the animal is, the greater is the influence of very low humidity upon its temperature. From their observations on the salamander, the frog, the toad, the lizard, the horned toad, the turtle, and the alligator, they draw the interesting conclusion that "possibly the increased ability of water retention evolved in the reptiles is a 'milestone' on the road to homoiothermism." We would suggest that before such a general conclusion can be drawn, one should study somewhat more completely the relative water content in the tissues of these animals. It could readily be argued that the armorlike plating of the skin of the alligator or the hard shell of the turtle would make for a decreased influence of humidity upon water vaporization, but the actual percentage of water in the tissues undoubtedly must be taken into consideration.

In our collection of rectal-temperature measurements on snakes, extending over several years, a large number of observations were obtained<sup>4</sup> that were unaffected by agitation and transition in environmental temperature and, in so far as possible, unaffected by handling, since the snake was left in its box and its tail alone pulled out for the measurement. These rectal temperatures have been averaged for the different 5-degree intervals of environmental temperature between 15° and 35° C. and the results are recorded in table 7. Practically all these temperatures, both rectal and environmental, were taken with the mercurial thermometer and the niceties of control of the thermo-junction method were not observed. In 63 observations between 15° and 20° C. the rectal temperature was usually somewhat greater than the environment, on the average 0.13°

<sup>1</sup> Soetbeer, F., Arch. f. exper. Path. u. Pharm., 1898, **40**, p. 53.

<sup>2</sup> See, also, the literature citations on this subject by Pembrey in Schafer's *Text-book of Physiology*, London, 1898, **1**, p. 793.

<sup>3</sup> Hall, F. G., and R. W. Root, Biol. Bull., 1930, **58**, p. 52.

<sup>4</sup> See the observations recorded on page 163.

greater. At all the other environmental temperatures from 20° to 35° the rectal temperature was lower than the environment. It is clear from our previous discussion (page 60) that the lower the temperature of the environment the greater may be the influence of the handling of the snake by the operator. It is believed, therefore, that the slightly plus value of 0.13° in the temperature interval between 15° and 20° may be fully explained by the heat obtained by the snake from the hands of the operator. These general averages confirm the more accurate study made with the thermo-junction method when the snake was extended in a wire-mesh tube, to the effect that the rectal temperature of the snake is lower than the temperature of the environment.

TABLE 7—Average differences between rectal and environmental temperatures in observations with snakes

Number of observations	Environment	Rectal temp. greater (+) or less (-) than environment
	°C.	°C.
63	15.01—20.00	+0.13
115	20.01—25.00	— .05
97	25.01—30.00	— .13
69	30.01—35.00	— .19

Fish, although surrounded by an ideal heat-absorbing medium (water), have been found to have a body temperature somewhat above the temperature of the environment.<sup>1</sup> It is to be questioned whether this higher body temperature represents a normally existing condition or whether it is caused in large part by the exercise and agitation incidental to catching the fish. Thus, Britton<sup>2</sup> has reported comparisons of the rectal temperature of fish and the temperature of the water, which show that fish taken at a depth of from 2 to 17 fathoms had on arrival at the surface a rectal temperature from 0.4° to 0.9° C. above that of the deep water. Fish kept in the laboratory tanks had a rectal temperature only insignificantly higher than that of the tank water, from 0.1° to 0.3° C. Possibly here again the activity prior to and during capture contributed to this temperature rise.

#### RECTAL TEMPERATURE AS AFFECTED BY CHANGES IN ENVIRONMENTAL TEMPERATURE

From the preceding discussion it would seem that the rectal temperature of the snake adjusts itself to the temperature of the environment and remains generally somewhat lower than that of the environment. This property of cold-blooded animals makes them especially adaptable for studying the rapidity with which temperature adjustments of this kind

<sup>1</sup> Simpson, S., Proc. Roy. Soc. Edin., 1907-8, **28**, p. 66; *ibid.*, Journ. Physiol., 1907-1908, **36**, p. xlii.

<sup>2</sup> Britton, S. W., Contrib. to Canadian Biology, Studies from Biol. Stations of Canada, N. S., 1923, **1**, p. 415.

can be made.<sup>1</sup> Sudden transitions in the temperature of the environment should affect the rectal temperature. To what degree and with what rapidity this effect takes place is a matter of interest. One of our earliest observations on this point was obtained on a 5-meter python (No. 2) at the New York Zoological Park. As already pointed out on page 55, this snake was taken out of its den by five men and its rectal and mouth temperatures were recorded in less than 3 minutes. These were 26.9° and 26.4° C., respectively. The snake was then carried outdoors from the reptile house to the primate house. This required 10 minutes, during which the python was exposed to an outside temperature of 0.5° C. Body temperatures, rectal and mouth, taken immediately upon arrival at the primate house, were 24.3° and 24.4° C., respectively. There was therefore a fall of 2.6° in the rectal temperature and 2.0° in the mouth temperature. That the temperatures did not fall more is explained in part at least by the agitation and struggle of the snake and by the heat given up by the warm hands of the five men. In any event, we have here a rapid fall in 10 minutes of approximately 2.6° C. in the body temperature of this snake. It would have been interesting to note what would have been the rate of cooling of a dead snake, if its initial body temperature had been 26° and it had been exposed for ten minutes to an environmental temperature of 0.5° C. The fall in body temperature probably would have been somewhat greater in the case of the dead snake, for there would be no internal factor of vital activity and the cooling effect of the environment would not be offset, as in the case of the live snake, by a production of body heat resulting from agitation and handling.

Later in our research (April 16, 1918) a more accurate study of the influence of sudden changes in environmental temperature was carried out on a boa. The boa had been kept in a chamber overnight, lightly covered with a blanket, and the temperature of its environment was accurately determined to be 30.6° C. At 1<sup>h</sup>07<sup>m</sup> p.m. the next day the boa was uncovered and, while it was still in the chamber, its rectal temperature was taken. The snake was then placed upon the floor of the laboratory. The temperature of the floor registered 20.2° throughout the entire afternoon and the room temperature remained between 21.5° and 22.0° throughout the entire experiment, which lasted from 1<sup>h</sup>07<sup>m</sup> p.m. until 5<sup>h</sup>50<sup>m</sup> p.m. While the boa was on the floor, rectal temperatures were taken fairly

<sup>1</sup> Although working with much smaller animals than we did, including clams, earthworms, salamanders and goldfish, Rogers and Lewis (Biological Bulletin, 1916, **31**, p. 1) found that the earthworm and the small salamander rapidly adjust their body temperature to that of their environment, but that clams and goldfish require a much longer time for the adjustment. They conclude that in the forms studied there is evidently no mechanism for the regulation of heat production or heat loss from the body, since such heat as is produced in the body is at once given off to the surrounding medium. Bohr (Skand. Arch. f. Physiol., 1904, **15**, p. 23) thought that the viper that he studied should be kept *for several days* at the temperature at which it was to be measured during the experiment. Therefore he is much against rapid shifts in temperature. Krüger (Zeitschr. f. Morphol. u. Ökolog. d. Tiere, Abt. A., 1931, **22**, p. 759) likewise discusses the relationship between the environmental and the body temperature of cold-blooded animals.

frequently. There was a regular, persistent fall in temperature until, at 5<sup>h</sup>50<sup>m</sup> p.m., the rectal temperature had reached 20.49°, at which time the experiment stopped. The data are given in detail in table 8. Much the same picture was noted in a preliminary experiment with a boa on April 14, 1918, which showed a rapid cooling in rectal temperature as a result of placing the boa on the floor. The data are much less complete and simply confirmatory of the general picture. Both series of observations show the pronounced effect of a sudden change in environmental temperature and the tendency of the snake to adjust itself (in the experiment of April 16, 1918, in about 5 hours) to a different environmental temperature.

TABLE 8—*Effect on rectal temperature of transferring boa from a chamber at 30° to a floor at 20° C.*

Time	Temperature of—	
	Rectum	Environment
p.m.	°C.	°C.
1 <sup>h</sup> 07 <sup>m</sup>	.....	30.59
1 09	30.19	.....
1 15	.....	20.29
1 19	27.81	.....
1 29	27.62	.....
1 39	26.67	.....
1 51	25.72	.....
2 01	25.18	.....
2 15	24.69	.....
2 34	23.56	20.20
2 50	23.30	.....
3 07	22.88	.....
3 28	22.28	.....
3 56	21.88	.....
4 16	20.99	.....
4 40	20.88	.....
5 20	20.55	.....
5 50	20.49	20.20

In this type of experiment there is always the difficulty of being certain that the temperature of the environment as registered by the mercurial thermometer is precisely that in contact with the snake.

In a series of experiments made in March 1920, there were a few instances when a snake (boa N) was either purposely or inadvertently removed from the environment in which it had been living for some time and placed suddenly in an environment having a markedly different temperature. In these instances the rectal temperature was measured repeatedly at 10- or 15-second intervals to note the rate of change in body temperature in the new environment. On March 1 in the morning, when the temperature of the snake's chamber was 15.50° C., the rectal temperature of the snake was 15.53° C. Eight hours later the temperature of the environment was approximately a half degree lower and that of the rectum was 15.07°, representing a close approximation to the change in environmental temperature. On March 3 at noon the temperature of the environment was 26.35° and that of the rectum 22.60° C. In the after-

noon the environmental temperature was  $27.10^{\circ}$  and the rectal temperature had risen to  $23.60^{\circ}$  C. In this particular case the boa had been at a lower environmental temperature the day before, nearer  $14^{\circ}$ , and we have undoubtedly to deal here with the natural rise in body temperature in keeping with the higher environmental temperature. On March 4 the temperature of the environment in the morning was  $31.60^{\circ}$  and that of the rectum  $28.56^{\circ}$  C. Five hours later the environmental temperature was  $28.90^{\circ}$  and the rectal temperature  $25.70^{\circ}$ . Even with relatively small changes in temperature of the environment therefore the snake's body temperature seeks the level of the environmental temperature, although as our results thus far presented have shown, the temperature of the snake is usually somewhat lower than that of the environment.

A more quantitative study to determine at what rate and to what degree the snake's internal temperature adjusts itself to the change in external temperature was carried out in the spring of 1918. From these experiments it may be determined whether the rectal temperature approximates the environmental temperature any more rapidly when the snake must adjust itself to a higher environmental temperature than it does when the snake must adjust itself to a lower environmental temperature. Special provision was made to insure that the snake's rectal temperature had attained a constant level in a given environment. The environmental temperature was then suddenly changed. After the snake had been living for a time at a warm temperature it was suddenly placed in a cold environment and after staying in the cold environment for a while, it was changed again to a warm environment. Four series of such experiments were carried out, two boas being studied almost simultaneously in two respiration chambers from March 24 to April 4, 1918, and from April 7 to April 14, 1918. The results are given in figures 18 to 21.

In figure 18 it can be seen that in the observations from March 24 to April 4 the rectal temperature (full-line curve) rose with the environmental temperature (broken-line curve) but was below the environment at the beginning of the experiment. When the temperature of the environment was suddenly dropped to  $15^{\circ}$  C., that of the rectum rapidly followed it but did not reach the same level or approximately the same level for nearly 24 hours. The environmental temperature was not held constant for any length of time, as is shown by the broken line. In general the rectal temperature followed the environmental temperature, although lagging behind and usually below it. At no stage of this particular experiment was the environmental temperature sufficiently constant for the snake to be considered to have been at a uniform temperature for 24 hours.

In figure 19 are recorded the results of another series of observations made with another boa in another chamber during the same period of time, from March 24 to April 4. The rectal temperature at the start was slightly above the environment, although the environment was fairly constant. At 10 a.m., March 26, there was a sudden rise in the environmental temperature, and the rectal temperature rapidly followed it, but



with somewhat of a lag. There was inadvertently a tremendous increase in the temperature of the environment at 8<sup>h</sup>30<sup>m</sup> a.m., March 30, followed by a marked decrease. With each fluctuation in environmental temperature there was also a fluctuation in rectal temperature. When the temperature

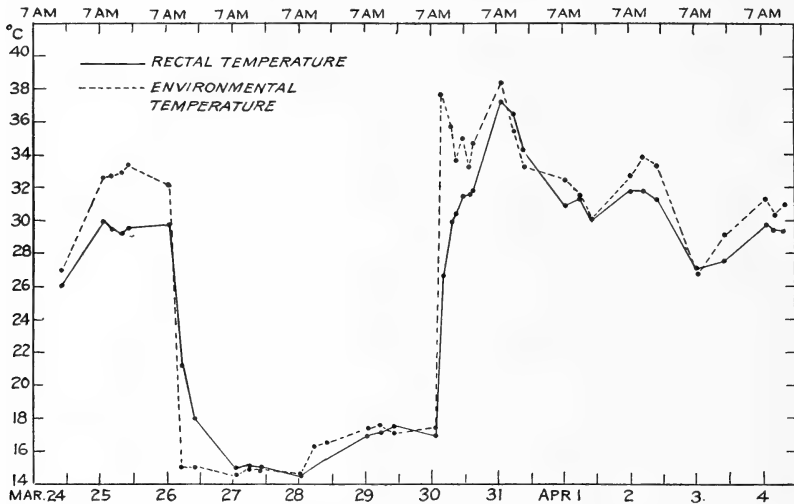


FIG. 18—INFLUENCE OF CHANGES IN ENVIRONMENTAL TEMPERATURE UPON RECTAL TEMPERATURE OF SNAKE.

Full-line curve represents rectal temperature and broken-line curve environmental temperature. Snake was removed entirely from its box each time rectal temperature was recorded in this series of measurements.

of the environment fell suddenly, the snake's body temperature was above it, but except during the periods of striking change the rectal temperature remained below the environmental temperature. From 8<sup>h</sup>30<sup>m</sup> a.m., March 31, until the end of the experiment there was a period in which the environmental and the rectal temperatures changed but little. During this period, however, the rectal temperature for the greater part of the time was a little above the environmental temperature, although both were not far from 18° or 19° C. During this period of seemingly constant temperature, each time the snake's temperature was measured, the snake was taken out of its box into a room invariably a degree or two warmer than the rectal temperature. This warmer room temperature and the necessary handling of the snake would tend to increase the snake's body temperature.

To obviate the effect of handling the snake, a change in the technique was made at the end of the second series of experiments on April 4, and in the next two series of experiments from April 7 to 14 the snake was not taken entirely out of the chamber when the body temperature was recorded, but the tail alone was pulled out and the thermometer (mercurial) inserted. Any handling of the snake was thus confined to the small area below the cloaca. Furthermore, the control of the environmental temperature was bettered so that the extreme fluctuations noted in the first two series of

experiments (figs. 18 and 19) were not experienced. The results of the observations from April 7 to 14 are recorded in figures 20 and 21.

In the experiment charted in figure 20 the cycle of temperature changes presents much the same picture as shown in figures 18 and 19. At both

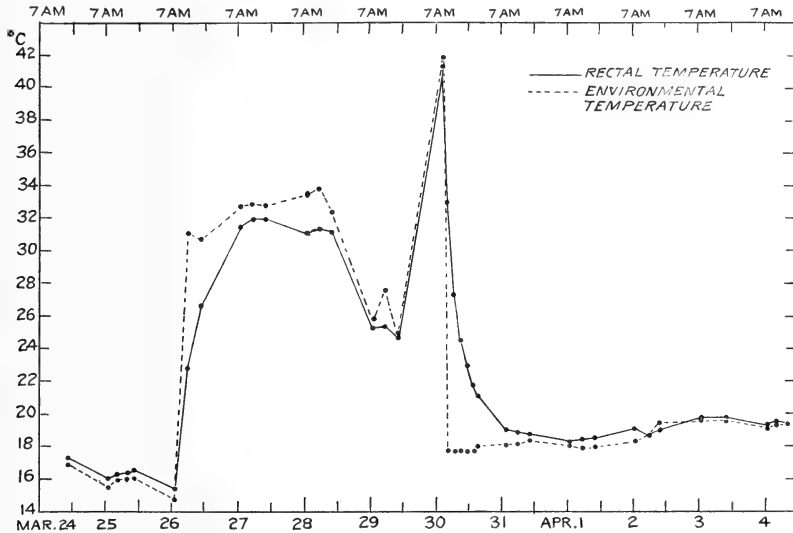
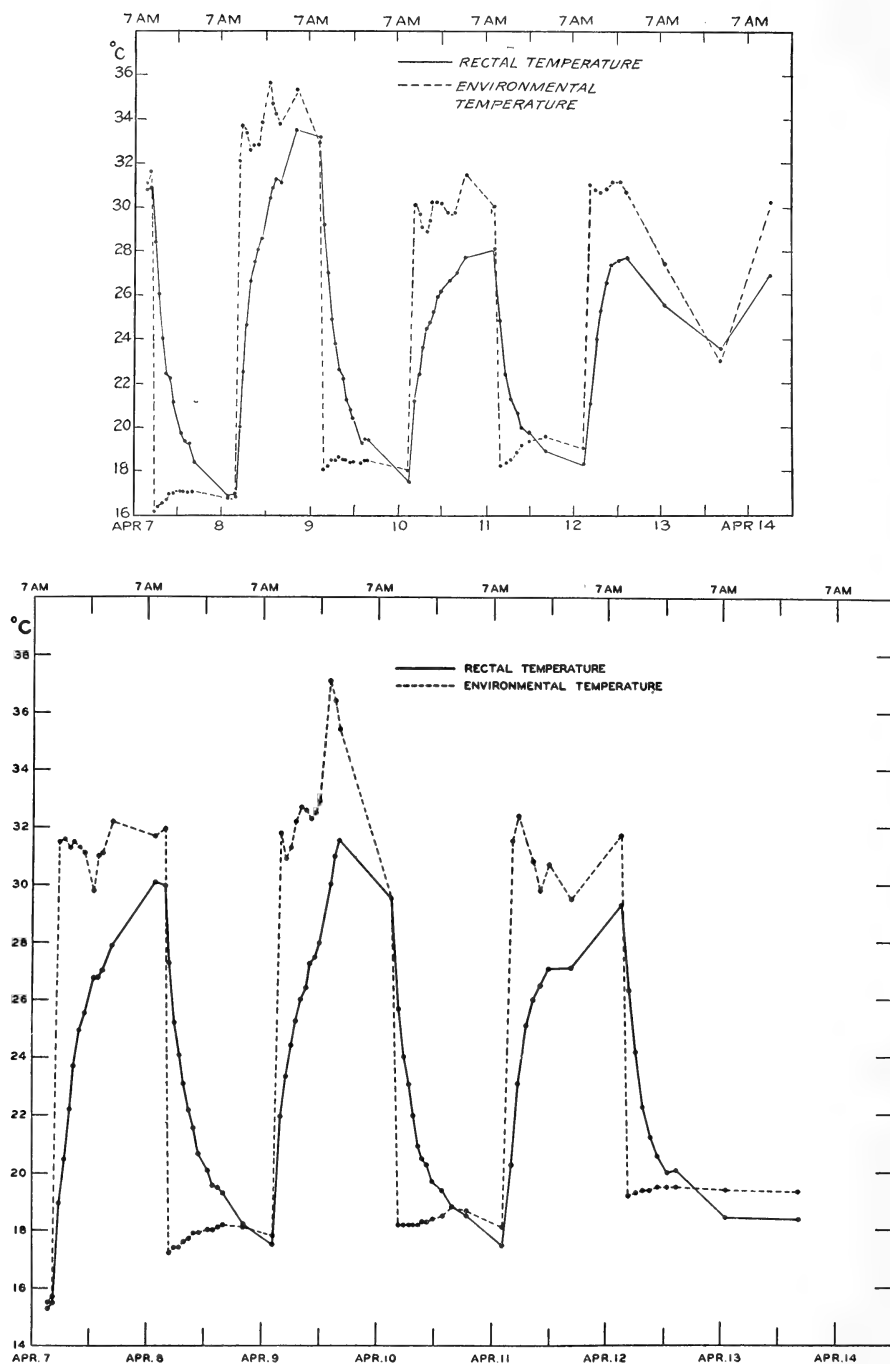


FIG. 19—INFLUENCE OF CHANGES IN ENVIRONMENTAL TEMPERATURE UPON RECTAL TEMPERATURE OF SNAKE.

Full-line curve represents rectal temperature and broken-line curve the environmental temperature. Snake was removed entirely from its box each time rectal temperature was recorded in this series of measurements.

the high and low temperature levels the rectal temperature after the period of transition was in most cases distinctly lower than the environmental temperature. The one exception occurred at 11<sup>h</sup>15<sup>m</sup> p.m., April 13, when the rectal temperature was above the environmental temperature.

In the experiment charted in figure 21, after two observations were made at the low temperature, *i.e.*, about 15°, there was a sudden change to nearly 32° C. in the environment and the temperature of the snake rapidly rose. The last two records of rectal temperature at the high level on April 8, two hours apart, were seemingly constant and measurably lower than the environmental temperature. The temperature of the environment was then suddenly dropped. The rectal temperature also fell, although slowly, and at the end of about 24 hours it was lower than the environment. The snake was again subjected to a warm environment and the rectal temperature began to ascend, but with a lag. After 8<sup>h</sup>58<sup>m</sup> p.m., April 9, there was a drop in environmental temperature in two stages and an immediate response in the rectal temperature. When the most pronounced drop in environmental temperature occurred, there was a lag in the response of the rectal temperature, but after 24 hours at the lower level the rectal temperature at 9<sup>h</sup>15<sup>m</sup> a.m., April 11, was



FIGS. 20, 21—INFLUENCE OF CHANGES IN ENVIRONMENTAL TEMPERATURE UPON RECTAL TEMPERATURE OF SNAKE.

Full-line curve represents rectal temperature and broken-line curve the environmental temperature. To avoid influence of handling, when body temperature was recorded snake was not removed from its box but the tail alone was pulled out and thermometer inserted in rectum.

measurably below the environmental temperature. In the third cycle of observations the environmental temperature was again increased. The rectal temperature followed slowly, but did not reach the same level. With the final rapid drop in environmental temperature there was likewise a rapid drop in rectal temperature and from 8 a.m. until 11<sup>h</sup>06<sup>m</sup> p.m., April 13, or for 15 hours, the rectal temperature remained at a constant level measurably below the environmental temperature.

The general picture to be drawn from figures 18, 19, 20 and 21 is that the rectal temperature of the snake remains below the environmental temperature when the temperature conditions are approximately uniform, without transition. When the environmental temperature is suddenly increased, the rectal temperature tends slowly to seek the same level, but never reaches it and, indeed, is noticeably below it. When the environmental temperature is suddenly lowered, the rectal temperature remains above it at first, but in about 20 hours reaches the same level and finally passes below it. These observations made in 1918 are confirmed completely by the measurements made in March 1920, from which it was concluded that the rectal temperature of the snake, under conditions where the temperature of the environment is not fluctuating, is below that of the environment, even at the lower temperatures. There is, however, a much greater difference between the rectal and the environmental temperature at the high levels than at the low levels.

Since the snake's body temperature reacts relatively slowly to changes in the temperature of the environment, if one wishes to be certain that the snake's body has attained a given environmental temperature, one must expose the snake for a long preliminary period to this temperature. This conclusion emphasizes again the criticism raised by various writers<sup>1</sup> against Vernon's first investigations,<sup>2</sup> that the temperature changes were too rapid. Kanitz<sup>3</sup> is of the opinion that Krogh's<sup>4</sup> experiments with the curarized dog are likewise subject to this criticism, that the temperature change was too rapid and that the recorded rectal temperature was probably not the temperature of the whole body.

#### INFLUENCE OF RAPID WIND MOVEMENT ON RECTAL TEMPERATURE

If the snake were to be considered as a wet bulb thermometer, it is conceivable that its body temperature would be lowered if a rapid current of air were blown over it. To contribute information regarding the problem of heat loss and the effect of vaporization of water, rectal-temperature measurements were made with two boas and a gopher snake during periods with and without wind movement. The snake was placed in a wire-mesh cage, open on all sides. This cage was put on the floor

<sup>1</sup>Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 614; Lindstedt, P., *Zeitschr. f. Fischerei*, 1914, **14**, p. 193; Kanitz, A., *Die Biochemie in Einzeldarstellungen, I.: Temperatur and Lebensvorgänge*, Berlin, 1915, p. 139.

<sup>2</sup>Vernon, H. M., *Journ. Physiol.*, 1895, **17**, p. 277; *loc. cit.*, 1897, **21**, p. 443.

<sup>3</sup>Kanitz, A., *loc. cit.*, p. 148.

<sup>4</sup>Krogh, A., *Internat. Zeitschr. physik-chem. Biol.*, 1914, **1**, p. 491.

of the laboratory under a table. Over the table was spread a blanket, which fell to the floor on both sides of the table. The ends of the table were only partly covered by the blanket, so that, by placing an electric fan directly facing one end of the table, the air set in motion by the fan would pass as if through a tunnel under the blanket, under the table, through the wire-gauze cage, and over the snake. The observations made under these conditions are by no means as complete as could be wished, but they are of interest.

The first experiment was made with a boa that had been for several days in a calorimeter chamber at an environmental temperature such that its rectal temperature was not far from  $23.5^{\circ}$  C. Indeed, the rectal temperature of this snake at  $2^{\text{h}}30^{\text{m}}$  p.m. on March 12 in this respiration chamber was  $23.85^{\circ}$  C. - The boa was then put in the wire-gauze cage mentioned above, and placed under the table with an electric fan running at slow speed. A mercurial thermometer was hung in the draft of air just after the air passed the cage. The rectal temperature, taken every half-hour thereafter (as shown in table 9), was at first high, undoubtedly reflecting the high rectal temperature of  $23.85^{\circ}$  at  $2^{\text{h}}30^{\text{m}}$  p.m. The snake was apparently endeavoring to seek the temperature of the environment. The rectal temperature slowly fell and at 6 p.m. was slightly lower than the environmental temperature. It remained essentially constant from 6 p.m. until midnight. It was impossible to control the temperature of the room perfectly, and there was a rise in the temperature of the environment beginning at 5 p.m. and continuing steadily until  $6^{\text{h}}30^{\text{m}}$  p.m. Although the snake's temperature had been falling prior to 5 p.m., it immediately began to mount. Between  $6^{\text{h}}30^{\text{m}}$  p.m. and midnight the environmental temperature fell  $0.6^{\circ}$  and the rectal temperature also fell. The boa was left in the wire-mesh box overnight, with a fan blowing over it steadily, but the temperature of the room was not controlled. The next morning at 8 a.m. the rectal temperature was  $21.48^{\circ}$  and the temperature of the air was  $21.38^{\circ}$  C. In other words, even after 8 hours in a blast of air at a temperature of not far from  $21.40^{\circ}$ , the rectal temperature had not appreciably altered. This shows that there was not a continuous cooling effect. The speed of the fan was increased to full speed at 8 a.m., March 13. The snake was not disturbed but was left in the box throughout the day until 3 p.m., observations being made hourly. The rectal and the air temperatures at 3 p.m. were essentially the same as at 8 a.m. Hence even when the animal was in a strong blast of air for 7 hours, there was no appreciable change in its body temperature. There was one instance when the air temperature went up, and this was followed by a rise in rectal temperature. On the other hand, when the environmental temperature fell, as in the latter part of the afternoon, the rectal temperature also began to fall. No more striking illustration of the reaction of these snakes to even small temperature changes could be given. It seems clear, therefore, that the strong blast of air affected the cold-blooded snake to a very slight degree. Unfortunately no measurements were made of the water

vapor under these conditions, but at least the heat-regulating device was not suddenly disturbed so as to alter appreciably the rectal temperature.

TABLE 9—*Influence of wind movement on rectal temperature of snake*

Snake and date	Time	Temperature of—		Ventilation
		Rectum	Environment	
1920		°C.	°C.	
Boa:				
Mar. 12. . . . .	2 <sup>h</sup> 30 <sup>m</sup> p.m.	23.85	23.50	Off
	3 00	22.40	20.72	On slow
	3 30	21.91	20.97	On slow
	4 00	21.67	21.27	On slow
	4 30	21.53	21.23	On slow
	5 00	21.53	21.32	On slow
	5 30	21.62	21.50	On slow
	6 00	21.71	21.87	On slow
	6 30	21.85	22.07	On slow
	11 59	21.33	21.43	On slow
Mar. 13. . . . .	8 00 a.m.	21.48	21.38	On slow
	9 00	22.25	22.98	On full
	10 00	22.34	21.73	On full
	11 00	22.12	22.27	On full
	12 00 noon	22.04	22.01	On full
	1 00 p.m.	21.91	21.81	On full
	2 00	21.55	21.40	On full
	3 00	21.41	21.38	On full
Gopher snake:				
Mar. 15. . . . .	5 00	20.70	20.12	On full
	11 30	20.22	20.48	On full
Mar. 16. . . . .	8 00 a.m.	18.80	18.02	Off
	10 00	22.74	22.88	On full
	12 00 noon	23.19	23.32	On full
	2 00 p.m.	22.88	23.12	On full
	5 00	24.08	24.25	On full
	8 00	23.68	23.53	On full
Mar. 17. . . . .	8 00 a.m.	21.59	21.53	Off
	10 30	22.35	22.68	On
	1 00 p.m.	21.68	22.00	On
	3 30	22.32	22.57	On
	5 00	22.14	22.20	On
	11 30	20.65	20.82	On
Mar. 18. . . . .	8 00 a.m.	17.71	17.62	Off
	10 00	19.71	20.31	On
	12 00 noon	19.95	20.11	On
	2 00 p.m.	20.08	20.16	On
	5 00	20.27	20.27	On
	11 00	21.29	21.38	On
Boa:				
Mar. 30. . . . .	12 00 noon	30.55	30.00	Off
	4 00 p.m.	20.42	19.00	On
	6 45	19.67	19.80	On
	10 45	18.91	18.87	On
Mar. 31. . . . .	1 40 a.m.	19.43	19.73	On
	8 00	18.78	19.32	On
	11 00	18.97	19.42	On
	2 00 p.m.	19.61	20.12	On
	5 30	20.42	20.92	On
	11 45	20.63	20.92	On

Another series of experiments was made with a gopher snake under exactly the same conditions. On March 15 a gopher snake was put in the cage under the table at 3<sup>h</sup>15<sup>m</sup> p.m., with the fan blowing over it at full speed. The first rectal temperature measurement was made shortly after 5 p.m. and registered 20.70° C. Supplementing the thermometer used in the experiment of March 12 to 13, we placed a temperature recorder on top of the wire-gauze cage directly in line with the air blast. This recording thermometer usually agreed within one- or two-tenths of a degree with the mercurial thermometer, and hence the readings on the mercurial thermometer alone are reported in table 9. The temperatures were taken at 11<sup>h</sup>30<sup>m</sup> p.m., the ventilation was then shut off, and the snake allowed to remain quietly in the room. The next morning at 8 a.m. the rectal temperature had fallen to 18.80° and the room temperature at that time nearest the box was 18.02° C. After the observations at 8 a.m. the ventilation was started with the fan on full speed, and at 10 a.m. the rectal temperature was 22.74° and the air current 22.88° C. The ventilation continued until 8 p.m., when it was again stopped. At this time, in order to get further evidence with regard to the temperature of the snake, a hole was made in the middle of the top of the cage, so that a thermometer could be inserted to within 15 or 20 cm. of the snake, obviously likewise in the direct air current. The next morning, March 17, before the ventilation was started, the rectal temperature was read as 21.59° and the temperature of the cage by this new thermometer as 21.53° C. It was soon found that the thermometer in the cage and the thermometer in the air current registered nearly the same, within one- or two-tenths of a degree, so from 8 a.m., March 17, and thereafter only the thermometer in the cage is recorded in table 9. Comparisons of the rectal and environmental temperatures were made at intervals throughout the day on March 17, and the ventilation was again stopped at night. On the morning of March 18 the rectal temperature had fallen to 17.71° and the temperature of the cage to 17.62° C. With the starting of the fan again, the rectal temperature rose, in spite of the increased ventilation, but the temperature of the cage likewise rose. Several observations were made throughout this day, and the experiment was ended at 11 p.m., March 18.

Another series of observations was made with a boa that had been in a warm chamber for 24 hours at an environmental temperature of not far from 30° C. At 2<sup>h</sup>25<sup>m</sup> p.m., March 30, the snake was taken from the warm chamber and placed in the wire-gauze cage under the table, with air blowing over its body. The rectal temperature of this snake at 12 noon in the warm chamber was 30.55° C. (see table 9). At 4 p.m. or 4 hours later, when the snake was in the wire cage under the table, it was 20.42° C., but the environmental temperature had dropped 11 or 12 degrees. The experiment continued all that day, throughout the night, into the next day until 11<sup>h</sup>45<sup>m</sup> p.m., March 31. There were unavoidable fluctuations in the air temperature in the middle of the cage and, as formerly, the

snake's temperature tended to follow these fluctuations, slight though they were, showing extraordinary sensitivity to the environmental temperature.

A critical experiment was not made to determine the rectal temperature of the snake over a *long* period of time with no air blast and with an air blast. But the evidence seems clear that there can be no pronounced effect of the movement of air *per se*. The movement of air with normal human beings and warm-blooded animals has two distinct effects, the chief of which is to bring to the warm body a blast of cold air, where there is a large temperature gradient between the body, the skin and the air. Theoretically, one could imagine that the blast of air would likewise make for a greater and more rapid vaporization of moisture from the skin. This, however, has been shown not to be the case, for the nude human body with a blast of air over it does not lose more water than the body without the blast of air.<sup>1</sup> The actual mechanism of the loss of water from the skin of the snake, especially of snakes having a scaly skin and those of moister skin, presents a problem still to be investigated. The measurements reported in table 9 do, however, emphasize the important rôle that water vapor may have in temperature adjustment. Hence our study included observations on the water vapor lost from the body of the snake.

#### SPECIAL STUDY OF RECTAL AND SKIN TEMPERATURES WITH 1931 PYTHON INFLUENCE OF DIGESTION AND ENVIRONMENTAL TEMPERATURE UPON RECTAL TEMPERATURE

No feature of the study of the 1931 python promised at the start to be of greater importance than the attempt to establish whether there is a consistent difference between the cell or body temperature of the snake and the temperature of the environment. One would think that with an animal whose body temperature so closely approximates the temperature of the environment, the relationship between these two factors could be easily established. The difficulties of determining the rectal temperature of these cold-blooded animals have already been dwelt upon, namely, the fact that the mere physical resistance of the snake to handling results in mechanical work that profoundly affects the body temperature and the fact that when the snake is handled by the operator its body "steals" heat from the operator's hands, particularly at the lower temperatures. But the difficulty of securing the true rectal temperature of the snake may be nowhere near as great as that of determining the true temperature of the environment, for the environment of the snake (air) is subjected to large temperature changes. If the snake could be immersed in water, the problem would be far simpler.

The general picture of the observations in the Nutrition Laboratory series of snakes studied in New York was that the temperature of the snake's body is usually a little below that of the environment and, to express it in popular language, that the snake partakes more or less of the nature of a wet bulb thermometer. It is not unusual for the snake to have a temperature above that of the environment. This was shown to

<sup>1</sup> Benedict, F. G., and C. G. Benedict, *Biochem. Zeitschr.*, 1927, **186**, p. 278.



be definitely the case in periods of activity following agitation or handling. Is it possible for the body temperature by internal processes alone, uncontaminated by muscular activity, to rise above the environmental temperature? This condition seemed to be met best and perhaps only by the process of digestion. During the peak of digestion does the snake have a cell temperature above the environmental temperature? Prior to bringing the 1931 python from New York to Boston for respiration experiments and thanks to the ever cooperative spirit of Dr. Raymond L. Ditmars, a number of body temperature measurements were made on well-feeding pythons, including our so-called 1931 python, in the New York Zoological Park. The rectal temperature was determined by the usual method, a mercurial thermometer being placed in the rectum with a minimum amount of agitation of the snake and the observations made as rapidly as possible, in order to minimize the conduction of heat from the hands of the operator to the body of the snake. These snakes had been accustomed to being handled, were tractable, and through the skill of Keeper John Toomey, the rectal temperature was measured with no difficulty. But the determination of the true temperature of the environment was a problem. The floor of the ordinary python den, which may be either of wood or, as is frequently the case, of roofing gravel, has a temperature much different from that of the air a few centimeters above it. Indeed, on different parts of the floor of the den the temperature may vary greatly, depending upon the distance of that particular part of the floor from the steam pipes below the floor. It soon became clear that we had no certain knowledge as to the exact environmental temperature under which the snake was living prior to the taking of the rectal temperature. A number of body temperatures were measured under these conditions, however, and the results are recorded in table 10, from which it can be seen that the rectal temperatures were somewhat higher than the uncertain floor temperatures.

In the attempt to secure a more uniform temperature of the environment, one of the snakes was placed in a dry, galvanized iron ash barrel. The opening of the barrel was covered with cotton fabric, and the barrel was then placed on the floor of a cage in which three giant pythons were regularly exhibited. This floor was covered with gravel and its temperature could be determined with reasonable accuracy. The thermometer placed in the fabric covering the opening of the barrel indicated presumably the temperature of the air. After the python, which was in the digestive stage, had spent several hours in this barrel, the barrel was rapidly removed from the cage and placed on the floor of the reptile house. The tail of the python was lifted and the thermometer inserted. Under these conditions the snake's temperature for the most part seemed to be somewhat *above* that of the environment, but here again the presence of air currents from the main door of the reptile house made the comparison of the true rectal and environmental temperatures unsatisfactory, and another procedure was adopted.

At the Nutrition Laboratory, two galvanized iron wash tubs were secured. The bottoms were cut out and replaced with half-inch (12 mm.) wire mesh. A top or lid of the same kind of wire mesh that could be fastened down was provided for each tub. Along the side of the tub was soldered a slotted brass tube in which the thermometer could be placed, and thus the temperature of the tub and presumably of the air in the

TABLE 10—*Comparison of rectal and environmental temperatures of snakes during digestion*

Snake and date	Hours fasting	Temperature of—	
		Floor of den	Rectum
1930-1931		°C.	°C.
Snake 1:			
Dec. 8. ....	Fed Dec. 8	27.0	28.2
Dec. 9. ....	24 (?)	27.1	28.9
Dec. 10. ....	48 (?)	27.0	29.2
Snake 2:			
Dec. 11. ....	1	27.0	30.0
Dec. 12. ....	.....	27.0	30.0
Dec. 13. ....	.....	27.5	29.4
Dec. 15. ....	.....	27.1	30.4
Dec. 16. ....	.....	27.4	28.7
Dec. 19. ....	.....	27.2	29.0
Snake 3:			
Dec. 13. ....	1	27.5	29.1
Dec. 15. ....	.....	27.1	30.0
Dec. 16. ....	.....	27.4	29.0
Dec. 19. ....	.....	27.2	29.5
Snake 4:			
Feb. 10. ....	12	26.8	29.8
Snake 5:			
Feb. 10. ....	12	26.8	30.0
1931 python:			
Jan. 7. ....	24	26.9	27.0

<sup>1</sup> Well past the time when the stomach was empty and after there was indication that the intestinal content had been well cleared.

tub could be recorded accurately. These two tubs, thus adjusted, were sent to Dr. Ditmars at the New York Zoological Park. A well-feeding python at the peak of digestion was placed in each tub. The tubs were then suspended from one of the trees in the exhibition cage for large pythons, in order that there might be free circulation of air through them at a reasonably uniform temperature. At the end of the day the tubs were quickly removed from the exhibition cage, the temperature of the thermometer in each slotted tube was recorded, and the rectal tempera-

tures of the snakes were taken. This procedure, which necessitated the transportation of the tubs from the python cage outside to a horizontal ladder support in the reptile house, produced a change in the environmental temperature which, although hardly  $1^{\circ}$  or  $2^{\circ}$ , was still much greater than the possible difference that might have appeared between the temperature of the rectum and that of the environment. This procedure was therefore modified in that the tubs, instead of being placed in the exhibition cage, rested on the ladder in the reptile house overnight at a constant temperature, regulated by a thermostat. The next morning the environmental and the rectal temperatures were taken without moving the tubs. Under these conditions a large python was found to have a rectal temperature of  $24.2^{\circ}$  as compared with an environmental temperature of  $24.8^{\circ}$ , a small python of  $24.5^{\circ}$  as compared with  $24.8^{\circ}$ , and the 1931 python of  $29.8^{\circ}$  as compared with  $26.5^{\circ}$ . These observations were made on January 9. The snakes had been fed 3 days before. Details of this procedure are given primarily to point out that, although one would *a priori* expect a small difference between the rectal and the environmental temperature to be easily established, such evidence is by no means simple to obtain. This type of observation was repeated on February 10. One snake had a rectal temperature  $0.4^{\circ}$  below the environmental temperature and another snake  $0.2^{\circ}$  above. These results again accentuate the difficulty in this seemingly simple experimental procedure.

In subsequent observations on the 1931 python in Boston, its rectal temperature was recorded after nearly every metabolism experiment. When the snake had been left inside the insulated respiration chamber for several hours, the environmental temperature must have been uniform, but even under such conditions the record of the environmental temperature was not without possible error. The moment the cover of the respiration chamber was removed, the air current from the room, which naturally varied somewhat in temperature, might influence the thermometer in the chamber and might even influence the snake's body temperature. The measurements of the rectal and environmental temperatures of the 1931 python obtained at the end of the several respiration experiments are recorded in table 11. The average temperature of the rectum was  $29.54^{\circ}$  and that of the environment  $29.14^{\circ}$ , that is, the rectal temperature was on the average *above* the environmental temperature. Close examination of the data, however, shows that in ten instances the rectal temperature was actually *below* the environment, but that the python was fed at 5 p.m. on January 24 and the rectal temperatures on January 27, 28 and 31 were *much higher* than the environmental temperature. Indeed, if this period of digestive activity were ruled out, the temperature of the rectum would be on the average the same as that of the environment. Recognizing, as only the experimenter can who has actually been working upon this problem, the difficulties of accurately measuring both the rectal and the environmental temperature, we are confident that there is nothing in the

results obtained with the 1931 python to alter the general impression secured in the earlier observations that under ordinary conditions, not during digestion, the rectal temperature of the snake is slightly below that of the environment.

TABLE 11—*Rectal temperature of 1931 python*

Date	Temperature of—		Date	Temperature of—	
	Rectum	Environment		Rectum	Environment
1931	°C.	°C.	1931	°C.	°C.
Jan. 15	22.70	22.12	Feb. 4	38.70	37.40
Jan. 17	24.68	24.80	Feb. 6	33.10	31.30
Jan. 20	14.28	12.80	Feb. 10	18.90	18.50
Jan. 21	31.00	31.31	Feb. 13	30.62	31.60
Jan. 22	31.38	31.79	Feb. 18	29.42	31.20
Jan. 23	24.65	24.69	Feb. 19	33.08	33.70
Jan. 24 <sup>1</sup>	25.11	25.80	Feb. 20	36.20	35.20
Jan. 27	35.60	30.75	Feb. 21	36.10	36.10
Jan. 28	33.08	32.37	Feb. 24	37.90	39.80
Jan. 31	34.00	31.30	Feb. 26	17.30	15.75
Feb. 2	32.51	33.60			
Average temperature of Rectum 29.54; of Environment 29.14					

<sup>1</sup> Fed Jan. 24, after rectal temperature was taken.

#### INFLUENCE OF ACTIVITY

With the 1931 python, two series of measurements were made to study the possible influence upon the rectal temperature of activity or agitation resulting from handling of the snake. Do the pulling out of the snake's tail from its box, the insertion of the thermometer into the rectum, and the resistance of the snake to the forcible withdrawal of the tail make for a slightly increased muscular activity on the part of the snake and consequently a slightly higher cell temperature? To answer this question two series of observations were planned. In the first, on February 25, the snake was allowed to rest in a wire cage in the small respiration chamber, and an attempt was made to hold the temperatures of the room and the respiration chamber constant. The snake's tail was pulled out of the cage, and the rectal temperature was determined approximately every 15 minutes. At the same time the wet bulb and the dry bulb thermometers were read, as well as the temperature of the water bath of the insulated respiration chamber. This series of measurements was made at a temperature of about 30° C. The results are given in table 12. The rectal temperature rose steadily throughout the forenoon. The picture is by no means clear cut, however, since, although the temperature of the dry bulb thermometer in the room underwent no material change, the temperature of the thermometer on top of the wire cage in which the python rested rose fairly steadily throughout the day, as did the bath temperature for part of the time. At the end of the experiment the python had a rectal

temperature  $0.8^{\circ}$  above that at the start. The dry bulb temperature was a little lower than at the start, the temperature on top of the wire cage was the same as at the start, and the bath temperature was one degree higher. Although it is realized that the body temperature of the python was definitely affected by the uncontrollable changes in the temperature of the room, nevertheless it seems justifiable to conclude that there was a *slightly increasing* cell temperature as a result of the repeated handling and the consequent activity of the snake.

TABLE 12—*Effect of continued agitation on rectal temperature of 1931 python at a high environmental temperature (Feb. 25)*

Time	Environmental temperature				Rectal temperature
	Dry bulb	Wet bulb	Bath	Top of snake's wire cage	
	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$
9 <sup>h</sup> 00 <sup>m</sup> a.m. <sup>1</sup>	30.2	16.8		29.80	29.72
9 15	30.4	15.5	30.8	30.02	29.92
9 30	31.7	17.3	31.2	30.02	30.02
9 45	30.9	16.0	31.2	30.51	30.09
10 00	30.6	15.7	31.1	30.51	30.09
10 25	31.0	15.9	31.1	30.47	30.15
10 40	30.6	16.0	31.2	30.30	30.18
10 55	31.0	15.6	31.2	30.72	30.29
11 10	31.3	15.9	31.4	30.60	30.30
11 25	30.1	15.2	31.2	30.30	30.32
11 40	30.2	15.3	31.3	30.39	30.31
11 55	30.0	15.5	31.3	30.51	30.40
12 20 p.m.	30.3	15.3	31.4	30.63	30.48
12 50	30.1	14.7	31.6	30.80	30.59
1 20	28.1	13.8	31.8	30.74	30.58
1 35	27.1	13.4	31.6	30.51	30.55
1 50	27.2	13.8	31.7	30.23	30.50
2 05	29.5	15.5	31.8	29.80	30.51

<sup>1</sup> Snake on insensible perspiration balance when temperatures at 9 a.m. were taken.

<sup>2</sup> Temperatures recorded 7 minutes after snake was put in respiration chamber.

<sup>3</sup> Snake handled more roughly at 11<sup>h</sup>55<sup>m</sup> a.m. and thereafter than it was before this.

A second experiment of much the same type but at a lower temperature, nearer  $20^{\circ}\text{C.}$ , was made on February 27 (table 13). At this temperature the snake was extremely lethargic. In this particular experiment the python had been left in the laboratory room overnight, and the recording thermometer showed that the environmental temperature for the most part had been about  $20^{\circ}$  and fell below  $20^{\circ}$  only at 6 a.m. At 9 a.m. and thereafter the rectal temperature was read every 5 or 10 minutes. The thermometer was left in the rectum throughout the series of observations, so that the snake was not disturbed by continually pulling out the tail. But its sides were touched every few seconds with a stick in the attempt to cause the muscular activity of rhythmic contractions. It was found

difficult to control the temperature of the room at this low level. The temperature of the dry bulb thermometer increased from  $17.2^{\circ}$  to  $18.8^{\circ}$  C. The wet bulb thermometer was about  $12^{\circ}$  C. The rectal temperature was  $19.90^{\circ}$  at the start and, as the experiment progressed, it slowly fell and then slowly rose again. This particular experiment was entirely negative, that is, there was nothing to indicate that there was sufficient muscular activity resulting from the slight stimulus to alter measurably the rectal temperature when the snake was in the lethargic state predominating at the temperature of  $19.5^{\circ}$  C.

TABLE 13—*Effect of continued agitation on rectal temperature of 1931 python at a low environmental temperature (Feb. 27)*

Time	Environmental temperature		Rectal temperature	Time	Environmental temperature		Rectal temperature
	Dry bulb	Wet bulb			Dry bulb	Wet bulb	
a.m.	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$		$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$
9 <sup>h</sup> 00 <sup>m</sup>	17.2	11.5	19.90	10 <sup>h</sup> 05 <sup>m</sup>	18.8	12.6	19.30
9 05	16.4	11.3	19.65	10 10	18.3	12.0	19.38
9 10	17.0	11.6	19.60	10 12	....	....	19.48
9 15	18.1	12.3	19.60	10 14	....	....	19.35
9 20	18.3	12.4	19.59	10 15	18.8	12.4	19.32
9 25	18.2	12.3	19.50	10 20	18.8	12.3	19.40
9 30	18.0	12.0	19.41	10 25	18.5	12.1	19.45
9 35	18.5	12.5	19.40	10 30	18.3	12.0	....
9 40	18.7	12.4	19.44	10 35	18.1	11.9	19.50
9 45	18.5	12.4	19.38	10 40	18.2	12.0	19.50
9 50	18.6	12.5	19.36	10 45	18.3	12.1	19.50
9 55	18.6	12.5	19.34	11 00	18.0	11.6	19.50
10 00	18.7	12.6	19.32	11 10	17.2	11.2	19.50

#### INFLUENCE OF DIGESTION UPON RECTAL AND SKIN TEMPERATURES AT A HIGH ENVIRONMENTAL TEMPERATURE

In the late afternoon of January 27, following a respiration experiment at an average temperature of  $31.9^{\circ}$  C., the 1931 python was found to have a rectal temperature of  $35.6^{\circ}$  when the environmental temperature was apparently  $30.7^{\circ}$  C. As a result of this challenging observation a survey of the snake's skin temperature was made, to determine whether there was on the body surface a local hot spot caused by the development of heat resulting from the digestive processes. As can be seen from table 11 (page 81), the difference between the rectal and the environmental temperature is greater during the digestive period than at any other time.<sup>1</sup> After the python had eaten two guinea-pigs on January 24, there was a distinct local swelling in its body. It was thought that because of the active process of digestion or disintegration going on and because of the normally slow circulation of blood in the long-drawn-out body of the serpent, there might be a local development of heat in the snake's digestive tract that would not be rapidly equalized. It was impossible to insert a thermometer down the gullet or up into the intestinal tract far enough to reach this point of supposed local heat development, but the problem

<sup>1</sup> See discussion on incubating python, page 86.

was studied in another way. With the thermo-junction already described (see page 43) a series of surface temperature measurements was made on January 28 and again on January 29, that is, 4 and 5 days, respectively, after the guinea-pigs had been eaten and after the snake had been resting quietly for some time in a reasonably uniform environmental temperature. The thermo-junction was applied to different parts of the snake's body, usually about every 15 cm. along its length, and special attention was paid as to whether there was any noticeable increase in skin temperature as the thermo-junction approached or receded from the large swelling of the body indicating where the guinea-pigs were being digested. The results are given in table 14. The snake was fed on January 24.

The rectal temperature taken just prior to the skin temperature survey on January 28 was found to be  $34.23^{\circ}$  or a full degree higher than the environmental temperature of  $33^{\circ}$  C. This suggests that at the temperature of  $33^{\circ}$  the snake is nearing the optimum temperature to lose its heat. As a matter of fact, it was found that this python's heat production on the day before, January 27, was very large as a result of the digestive processes and the high environmental temperature. Therefore, the interpretation might be that the snake was actually overheated when the rectal temperature of  $35.6^{\circ}$  was noted on January 27. During the respiration experiment on January 27 the air was passed into the respiration chamber directly from outdoors, that is, not dry, and undoubtedly a considerable amount of moisture entered the chamber with the outdoor air. At one time the glass tube of the rotamesser in the ventilating system actually became fogged, and the rate of ventilation had to be increased. Between the sixth and the seventh periods, two calcium-chloride tubes were inserted in the line preceding the respiration chamber and during the next three periods of the experiment the outdoor air was dried before entering the chamber. Under these conditions there was a more favorable opportunity for the snake to vaporize water and thus control its body temperature. But even so, the high rectal temperature of  $35.6^{\circ}$  was found. On January 29, therefore, during the respiration experiment preceding the skin temperature survey, the outdoor air entering the respiration chamber was dried the entire time. This made more favorable conditions for the snake to lose its body heat and regulate its temperature.

In general the skin temperatures were slightly higher on the larger parts of the body and lower near the tip of the tail and the top of the head. That this difference in temperature could be attributed to the local digestive processes is, however, difficult to say. The environmental temperature in this skin temperature survey was between  $32^{\circ}$  and  $33^{\circ}$ . The rectal temperature was more nearly  $34^{\circ}$ , and the skin temperature was likewise more nearly  $34^{\circ}$ . The skin temperature on the whole was a little below the rectal temperature, although parts of the skin showed essentially

<sup>1</sup> Thermo-junction without insulation in this series.    <sup>2</sup> Wet bulb,  $17.9^{\circ}$  C.

<sup>3</sup> On lump where guinea-pigs were being digested.

<sup>4</sup> Thermo-junction protected with hard-rubber cover.    <sup>5</sup> About 10 cm. from tail, on top of snake.    <sup>6</sup> Room temperature determined by thermo-couple,  $34.06^{\circ}$  near lump and  $34.0^{\circ}$  near head of snake.    <sup>7</sup> Near the lump.    <sup>8</sup> Beneath belly and lump.    <sup>9</sup> On belly, near lump.    <sup>10</sup> On belly and on back.    <sup>11</sup> Wet bulb,  $20.1^{\circ}$  C.

TABLE 14—*Influence of digestion upon rectal and skin temperatures of 1931 python\**

Date and time	Temperature of—		Location on skin	Skin temperature
	Room	Rectum		
1931	°C.	°C.		°C.
Jan. 28:			Between folds <sup>1</sup>	
4 <sup>h</sup> 28 <sup>m</sup> p.m.	23.00	34.23	15 cm. from nose.....	34.00
4 29			45 cm. from nose.....	34.13
			60 cm. from nose.....	34.00
			76 cm. from nose.....	33.81
			91 cm. from nose.....	34.13
4 30			107 cm. from nose.....	34.06
			122 cm. from nose.....	34.25
			137 cm. from nose.....	34.25
4 31			152 cm. from nose.....	34.44
			168 cm. from nose.....	34.19
			183 cm. from nose.....	34.32
			198 cm. from nose.....	34.00
4 32	33.00		On top of folds <sup>4</sup>	
4 35			Head, 4 cm. from nose.....	33.81
			15 cm. from nose.....	33.68
			30 cm. from nose.....	33.81
			45 cm. from nose.....	33.94
4 36			60 cm. from nose.....	33.87
			76 cm. from nose.....	33.94
			91 cm. from nose.....	33.87
			107 cm. from nose.....	33.94
			152 cm. from nose.....	33.94
			183 cm. from nose.....	34.00
4 37			213 cm. from nose <sup>5</sup> .....	34.00
	6		Between folds, on belly, under lump <sup>1</sup> .....	34.32
			Between folds, on belly, under lump <sup>1</sup> .....	34.00
4 39			Tip end of tail.....	34.06
4 40			Beneath chin.....	33.94
			Between folds	
			Between belly and back, 15 cm. from nose.....	34.25
			Between two sides, 45 cm. from nose.....	34.25
			Belly, 60 cm. from nose <sup>7</sup> .....	34.44
4 41			Between folds, 76 cm. from chin <sup>8</sup> .....	34.32
4 42			Between two sides, 76 cm. from head.....	34.38
4 43			Between back and cage, 70 cm. from head.....	33.94
			Beneath cage, in middle of whole snake.....	34.13
4 44		34.32	Outside rectum, 2 cm. towards head.....	34.13
4 46	34.13		Outside rectum, 2 cm. towards tail.....	34.06
4 47			Against side, 90 cm. from head.....	34.25
			On top of folds <sup>4</sup>	
Jan. 29:			Top of head, 4 cm. from nose.....	33.08
4 35 p.m.		33.89	15 cm. from nose.....	33.34
			30 cm. from nose.....	33.60
			45 cm. from nose.....	33.40
			60 cm. from nose.....	33.60
			Over lump.....	33.47
			15 cm. below lump.....	33.60
4 36	132.43		30 cm. below lump.....	33.73
	132.63		60 cm. below lump.....	33.60
			75 cm. below lump.....	33.53
			90 cm. below lump.....	33.86
			105 cm. below lump.....	33.34
			Tip of tail.....	32.95
4 38			Between folds, 38 cm. from tail <sup>9</sup> .....	34.05
4 39			On belly, 30 cm. from head.....	34.24
			On back, 25 cm. from tail.....	34.24
			Between folds, 50 cm. from head <sup>10</sup> .....	34.31
4 41	31.91	34.21	Between sides, near tail.....	34.20
	32.69		Outside rectum, 1 cm. towards head.....	33.60
	132.24		Outside rectum, 1 cm. towards tail.....	33.53

\* See notes on page 84.



the same temperature as did the rectum. The fact that the skin temperature was obviously above the environmental temperature confirms the belief that during the digestive processes at least there is an increase in heat production sufficient to change the normal relationship between the temperature of the environment and that of the skin so that the rectal temperature, instead of being as usual a little below the environmental temperature, is above it.<sup>1</sup> Indeed, this study shows definitely that as a result of digestion not only is the snake's rectal temperature above the environmental temperature, but likewise its skin temperature.

The contribution of digestive activity to the heat economy of the serpent was strikingly illustrated by the behavior of the snakes in the large python den in the New York Zoological Park, noted in January 1931, at the time the observations of the rectal temperature during digestion were obtained. This den is approximately 20 feet (6 meters) wide and 35 feet (11 meters) long, and is heated by steam pipes running longitudinally through the center below the cement-gravel floor. It was observed on one occasion that two of the pythons were lying directly over the steam pipes in the center of the den, while a third python was lying at one side of the den and partly against the glass wall. The two pythons in the center had not fed for some time. The third python lying against the glass wall was in the active stage of digestion and obviously was sufficiently comfortable not to need extra heat from the steam pipes. Measurement of the temperature of the gravel on the floor where the third python was lying showed it was about 21° C. The temperature of the floor over the steam pipes, on the contrary, was 32° C.

#### COMPARISON BETWEEN ENVIRONMENTAL TEMPERATURE AND SKIN TEMPERATURE OF AN INCUBATING PYTHON

It has been pointed out in the preceding pages that the difficulty of obtaining a correct record of the environmental temperature may be as great, if not greater, than that of obtaining the snake's true body temperature. But it is nevertheless clear from the experience of the Nutrition Laboratory that in general when the snake is in repose, its rectal temperature is slightly below the environmental temperature and its skin temperature somewhat lower than the rectal temperature. These body temperatures, according to our experience, can be increased above the temperature of the environment only when the snake is at the peak of digestion or when it is agitated. Proper determination of the environmental temperature is difficult even with modern technique. This, together with the fact that the skin temperature of the snake, when in repose, is usually below rather than above the environment, led to a reconsideration of the classic reports on the incubating python, which state that the female python, after laying its eggs, coils itself about them and produces sensible heat to aid in the incubation. This current belief is based in large part upon the early observations of Valenciennes and the later determinations of Selater and Forbes. In March 1832, the French naturalist, Lamarre-

<sup>1</sup>Duméril (*Annales d. Sci. Nat., Zool.*, 1852, 3d ser., **17**, p. 5) early noted an increase in the body temperature of snakes after eating.

Picquot,<sup>1</sup> read before the French Academy a communication regarding the habits of serpents, in which he stated that there is a real incubation in the case of the python of Bengal. This report was turned over to a committee of the Academy for examination, and they rejected Lamarre-Picquot's statements as being hazardous and questionable. One of his statements dealt with the ability of a certain species of snake "to withdraw milk from the udder of a cow"!! No comments are made with regard to the matter of incubation in the account published in 1835 of Lamarre-Picquot's communication.

Subsequently Valenciennes<sup>2</sup> presented before the French Academy a communication regarding his observations on an incubating python. He studied a python which had laid eggs in the Jardin des Plantes in Paris. He was granted the privilege of making this study by Duméril, who had been and was at that time the most severe critic of the statements of Lamarre-Picquot. Valenciennes described carefully how the snakes were kept in the snake house and how they were heated from below by means of water vessels refilled with hot water from time to time. On May 6 the python laid 15 eggs. Apparently the snake had been covered with a cloth, and the eggs were laid under the cloth. When the eggs were laid, the python coiled about them so that it was impossible to see a single one. Prior to the laying of the eggs, the animal had been tranquil and tame, but after she had coiled about the eggs, it was dangerous to approach her. Valenciennes reports an extensive series of temperature measurements taken by means of mercurial thermometers (1) in the room, (2) under the cloth covering, and (3) between the folds of the snake and upon the eggs. On May 8, when the room temperature was 23°, the air under the cover had a temperature of 28.5° and the temperature between the folds of the animal and on the eggs was 41.5°. As time went on, the temperature between the folds of the snake decreased steadily until, on July 2, it was 28°. It was always, however, measurably above the room temperature and likewise measurably above the temperature under the cover. Valenciennes recognized that the imperfect method of heating from below may have had an influence upon these temperature differences and made some control experiments, which seemingly rule out completely the possibility of heat from the hot-water supply having had any great influence upon the animal itself. It is not clear from his discussion whether the snake was in a small box in which the air was more or less pocketed, or whether it was in one corner of a large cage with the possibility of considerable movement of air about it. In any event, a careful examination of the protocols leaves no doubt but what Valenciennes recognized the possibility of errors in determining the difference between the temperature of the environment and that of the snake and made every effort to overcome such errors. The largest difference between the air temperature and the temperature of the python was 21° (room temperature 20°; snake's temperature

<sup>1</sup>Lamarre-Picquot, *L'Institut*, 1835, **3**, p. 70.

<sup>2</sup>Valenciennes, A., *Compt. Rend.*, 1841, **13**, p. 126.

41°). This is the largest difference that has ever been noted under similar conditions. The fact that the animal showed a desire to drink during the incubation period and drank water with avidity is taken as an indication by Valenciennes that it was in a "state of fever."

In a short note published in 1842 Lamarre-Picquot<sup>1</sup> maintained that he had confirmed what he had previously stated with regard to the incubation of certain large Ophidians by observations made in Transylvania of a similar case. At the same meeting at which Lamarre-Picquot made this communication Duméril stated that he would shortly present to the French Academy a discussion of the observations of Lamarre-Picquot and Valenciennes. Later in the same year a communication was published by Duméril<sup>2</sup> dealing with the development of heat in the case of serpents and the influence attributed to the incubation by the mother. Duméril began this communication by referring to the earlier statement in 1832 of Lamarre-Picquot and to the controversy started at that time. He objected to the idea of the development of heat by the python comparable to a state of fever, on the grounds that the broken eggs and the matter excreted by the snake would ferment and this fermentation of itself would result in a considerable production of heat. Therefore he thought it had not been demonstrated that the snake actually produces sensible heat to aid in hatching the eggs. Duméril includes in his report a long abstract of a discussion on the procreation of serpents, their eggs, and the phenomenon of the development of heat, which was published in a book entitled *L'Erpétologie Générale*, by himself and Bibron. In spite of the care taken by Valenciennes in making his observations under the direction of Duméril, the latter believed that the experiments of Valenciennes were not conclusive, because there might have been a considerable source of heat from the bottom of the box in which the snake was studied, and the heat might not have been produced by the animal itself. Duméril repeated some of Valenciennes' experiments by placing vessels of warm water beneath the same apparatus employed by Valenciennes. A woollen cloth was placed in the apparatus, draped in a dome shape so as to have an empty space in the center of it. At the end of several hours two thermometers were placed in the apparatus, one outside the cloth and one in the empty space beneath the cloth. The latter thermometer indicated a temperature 10° C. higher than the thermometer outside the cloth, and Duméril concluded that the warm water in the water vessels was the source of the extra heat. At the close of this communication by Duméril, Dumas stated that he believed Valenciennes had used every reasonable precaution to guarantee the accuracy of his observations but that the comments of Duméril necessitated a new examination.

It was not until sixteen years later that Lamarre-Picquot presented another communication<sup>3</sup> to the Academy, in which he stated that he wished

<sup>1</sup> Lamarre-Picquot, *Compt. Rend.*, 1842, **14**, p. 164.

<sup>2</sup> Duméril, *Compt. Rend.*, 1842, **14**, p. 193.

<sup>3</sup> Lamarre-Picquot, *Compt. Rend.*, 1858, **47**, p. 525.

to modify an earlier statement in which he used the expression "incubation of Ophidians." This expression, he said, had been interpreted wrongly and had apparently led to the belief that he thought all animals of this species had the ability to produce heat to favor the incubation of eggs, whereas he meant the expression to apply only to certain large species of python and "anaconda" (sic). Immediately after Lamarre-Picquot had made this communication to the Academy, Duméril spoke and after criticizing Lamarre-Picquot's contention with regard to the possibility of the snake drawing milk from cattle, he made the following statement:

"Il est constaté d'autre part que les serpents, par suite même de leur mode de circulation et de respiration, ont une température variable comme celle du milieu dans lequel ils vivent; qu'elle s'abaisse par le froid et s'élève tellement par le chaud, que si la main vient à les saisir lorsqu'ils ont été exposés à une forte chaleur, elle a pu reconnaître quelquefois jusqu'à près de 60 degrés."<sup>1</sup>

A temperature of 60° is 19 degrees above the highest snake temperature observed by Valenciennes and would seem to be intolerable for a snake. The inaccuracy of using the hand as a thermometer to express the temperature in degrees is apparent.

A report of most careful observations on an incubating python made in the Gardens of the Zoological Society of London was published by Sclater in 1862.<sup>2</sup> The female python studied was one of the largest that this Zoological Society had ever had in captivity. It measured about 6.5 meters in length. Approximately one hundred eggs were laid during the night of January 12-13, 1862. The snake took a characteristic position, coiled completely around the eggs so as nearly to exclude them from view. Using especially accurate mercurial thermometers, Sclater made a series of temperature measurements on the surface and between the folds of the snake. To avoid, if possible, errors in determining the temperature of the environment, he measured not only the temperature of the female on the eggs but likewise of the male in the same den, on the assumption that any difference in temperature observable between these two animals would be attributable to the effect of incubation. The data obtained by Sclater, but converted from degrees Fahrenheit to degrees Centigrade, are given in table 15, from which it can be seen that at least at one time there was a difference of as much as 11° C. between the temperature of the male and that of the female. In general, the temperature of the air in the den was low, averaging 16.8° rather than the 30° commonly prevailing in snake dens at the present day. The temperature of the male was high in comparison with that of the environment, from 3.5° to 9° higher. This is a finding wholly out of accord with the observations secured by the Nutrition Laboratory on snakes in repose. The author states that on April 4 the eggs were evidently undergoing decomposition and gave forth a strong,

<sup>1</sup> Duméril, *Compt. Rend.*, 1858, **47**, p. 526.

<sup>2</sup> Sclater, P. L., *Proc. Zool. Soc.*, London, 1862, p. 365.

nauseous odor. A few of the eggs were fertile, containing small embryos, but the larger number of them contained only fatty matter in a state of decomposition. Slater concludes from his own observations, taken in conjunction with those of Valenciennes and a communication addressed to him by Wray,<sup>1</sup> that it is a normal habit of these Ophidians, the pythons, to incubate their eggs, much as in the superior class of birds.

Wray's communication referred to a letter received from a Colonel Abbott, who stated that in March 1838 a female python, some 3.5 meters in length, was removed from under a rock with a nest of 48 eggs. The snake was in his possession for upwards of two and a half months and was constantly coiled around her eggs. On leaving the town of Arracan for

TABLE 15—*Study of body temperature of an incubating python—Slater*<sup>1</sup>

Date	Tem- perature of air in den	Skin temperature			Differ- ence
		Location	Male	Female	
	°C.		°C.	°C.	°C.
Feb. 12	14.8	On surface. . . . .	21.2	22.8	1.6
		Between folds. . . .	23.8	27.6	3.8
Feb. 23	18.6	On surface. . . . .	22.1	24.1	2.0
		Between folds. . . .	23.3	28.4	5.1
Mar. 2	15.6	On surface. . . . .	22.0	28.9	6.9
		Between folds. . . .	24.4	35.6	11.2
Mar. 9	16.1	On surface. . . . .	22.7	26.4	3.7
		Between folds. . . .	<sup>2</sup>	30.3	....
Mar. 16	18.9	On surface. . . . .	22.4	25.3	2.9
		Between folds. . . .	25.3	30.0	4.7

<sup>1</sup>Slater, P. L., Proc. Zool. Soc., London, 1862, p. 367.  
<sup>2</sup>Not observed, the male being very restless.

Calcutta, Abbott took the snake and the eggs with him, but had to leave Calcutta before the eggs were fully hatched. This interesting communication suggests that it would be possible to study the gaseous metabolism of an incubating python while on her eggs, a study so keenly desired by Krogh.<sup>2</sup> Apparently the python is very loath to leave her eggs, and it

From the standpoint of our temperature studies, the results of Slater would not be an impossible procedure to transfer a python and her eggs to a respiration chamber and measure the gaseous metabolism.

are inexplicable because of the great difference between the temperature of the male python and the environment. If his measurements on the male python are true and there is this difference between the temperature of the environment and that of the male python, then it is a question whether the male as well as the female produces sensible heat. The observations of the Nutrition Laboratory on snakes in repose all point against this. Our direct calorimetric measurements (see page 423) rule out, at

<sup>1</sup>Wray, G. O., Proc. Zool. Soc., London, 1862, p. 108.  
<sup>2</sup>Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, p. 123.

least with the python and the boa during repose, the possibility of sensible heat being produced. It would thus appear as if the possibility of error in determining the true environmental temperature was not recognized sufficiently in Selater's experiments. His clever scheme of comparing the temperatures of the male and the female, on the assumption that the environmental temperature would be the same for both, is likewise unfortunately open to criticism, for it is more than likely that the two snakes were not near each other, as will be seen in subsequent discussion (see page 95) of the actions and habits of the male when the female is incubating eggs, and that the environmental temperature might have been markedly different for one than for the other. Furthermore, the possible source of heat from the large mass of fermenting eggs (100 or more, each about 7 or 8 cm. in diameter) must not be overlooked. For these reasons the observations of Selater are not, in our judgment, conclusive.

In 1881 another instance of incubation of an Indian python was observed at the London Zoological Park and reported by Forbes.<sup>1</sup> The snake, a *Python molurus*, about 3.5 meters long, produced during the night of June 5-6, 1881, about 20 eggs and coiled herself around them in the characteristic manner. In this position she remained for 6 weeks without once eating and with only one break in her incubation. On July 18, that is, 43 days after the eggs had been laid, the eggs were evidently decomposing and therefore were removed. Their state on examination was found to be similar to that observed by Selater on a previous occasion, that is, strongly decomposed. Forbes employed specially graduated mercurial thermometers for the temperature measurements and followed the same scheme adopted by Selater of determining the temperature both on the female and on the male. The male had been removed from the female when the eggs were laid and was kept in a cage next to that of the female, under practically identical conditions. The temperature of the snakes was measured by placing a thermometer on the surface of the body, then between the folds of the coils, but in each case the snake's body was covered by the blanket under which it usually rested. The temperature of the air was taken by suspending a thermometer a little way above the floor of the cage; that of the gravel in the cages by burying the bulb of the thermometer in the gravel in the same position in each cage and over the hot water pipes which ran beneath the floors of the cages. The temperature study extended from June 14 to July 18, observations being made practically every other day. Though the male was kept in another chamber, the temperature of the chamber air was much the same as that of the chamber in which the female was kept. The air temperature varied from 22.4° to 30.6° C. The temperature between the folds and on the surface of both snakes closely followed the temperature of the air, in accordance with the well-known adjustment of the snake's temperature to its environment.

<sup>1</sup> Forbes, W. A., Proc. Zool. Soc., London, 1881, p. 960.

Forbes has averaged all the temperature records of both animals and finds that on the average the temperature between the folds is higher than that on the surface. The average temperature on the surface of the male was  $28.3^{\circ}$  and on the surface of the female  $29.1^{\circ}$  C., the female's temperature being  $0.8^{\circ}$  higher. Between the folds the temperature of the male averaged  $30.0^{\circ}$  and that of the female  $31.7^{\circ}$ , or  $1.7^{\circ}$  higher. The individual records show that invariably the temperature between the folds was somewhat higher with the female than with the male. On several occasions the temperature on the surface was actually higher in the case of the male. The temperature of the air of the cage was usually lower than that of the air under the blanket, but that of the gravel was high, averaging  $29^{\circ}$  C.

In view of our own experienced difficulties in determining the true temperature of the environment, we are quite disposed to consider that this difficulty likewise entered into the experiments of Forbes. Furthermore, there is also the confusing factor of putrefying eggs. It is reasonably clear that the female python remains practically the entire time on her eggs and does not leave them, nor does she eat. The male ate at least once, and as these animals are of nocturnal habit, it is more than likely that he left his box and went outside a number of times. The undoubtedly greater vaporization of water when the animal was out from under the blanket would result in a somewhat lower body temperature. But the finding that the temperature of the male was many degrees above that of the air is, we believe, evidence of an error in establishing the true temperature of the environmental air.

Soetbeer,<sup>1</sup> in 1898, discussed the experiments of Valenciennes, Selater, and Forbes, and stated that he considered their findings problematical. In 1905 Doflein<sup>2</sup> had an opportunity to observe a specimen of the *Python molurus* in Colombo, brought there recently from the Malayan Archipelago. This python laid 100 eggs and coiled herself about them, in which position she remained for 11 weeks, without eating anything in this time. The young snakes finally came out of the shell, and he naïvely observes that "to his great astonishment in the evening they went back into their empty shells, about which the mother snake still lay coiled." (Sic!) In 1916 Krogh,<sup>3</sup> in his monograph on the respiratory exchange of animals and man, commented upon the experiments of Valenciennes and made the statement that he had had occasion to observe that the python is "especially quiet during the first period of incubation when the temperature is highest, and it appears unlikely that muscular movements should be at all responsible for the large increase in temperature." In a personal communication to the writer on May 20, 1931, Professor Krogh stated that he saw this brooding python at the Zoological Gardens in Copenhagen. The

<sup>1</sup> Soetbeer, F., Arch. f. expt. Pathol. u. Pharm., 1898, 40, p. 53.

<sup>2</sup> Doflein, F., Tierbau u. Tierleben, II: Das Tier als Glied des Naturganzen, 1914, Leipzig and Berlin, p. 593.

<sup>3</sup> Krogh, A., The Respiratory Exchange of Animals and Man, London, 1916, p. 123.

python had laid a large number of eggs and was coiled conically around them, with the head in the apex. The breathing was deep and regular, but otherwise the animal was very quiet. Preparations were made to determine the respiratory exchange of this snake but permission to do so was refused.

In 1929, during the course of the Chancellor-Stuart expedition of the Field Museum of Natural History, a photograph was taken of an incubating python (*Python reticulatus*) coiled around her eggs. A second photograph was taken of the eggs with the python removed. These are reproduced in figures 22 and 23. They were taken on the Upper Ogan River, Sumatra, by Dr. Philip M. Chancellor, and permission to reproduce them in this report was kindly given to us by Director S. C. Simms of the Field Museum of Natural History in Chicago. Nothing has been published thus far about this specimen, other than the reproduction of these photographs in the public press. The python was 8 meters long. No record was made of its weight.

FitzSimons, in his book on *Pythons and their Ways* (1930, pp. 14 to 16), mentions the incubating python, gives an illustration of one coiled about her eggs, and lists a number of records of the eggs laid by pythons of different size. He states that the number of eggs laid varies according to the size of the snake, that the mother python coils about the eggs in the form of a cone so that they are invisible, and that during the process of incubation her blood rises to a temperature of 90° F. (32.2° C.), "which is apparently Nature's rule for the hatching of infant pythons."

Our interest in the incubating python is far greater than the desire simply to know whether the eggs are incubating. Thus, we are interested to know whether it is possible for a large cold-blooded animal, such as the python, to produce sensible heat without muscular activity, without agitation, and without digestion. If this is true, then the incubating python represents an intermediary stage between the cold-blooded and the warm-blooded animals. If sensible heat is produced, there must be an alteration in the mechanics of heat production and heat loss. In some of the reports on incubating pythons, comments have been made with regard to their irritability and their tendency to defend their eggs from anyone who approaches. But the fact that temperature measurements could be made without difficulty over a period of several weeks or several months, as was the case in some of the observations reported in the literature, would imply that the incubating python is not excessively agitated, for if this were so, it would certainly have been recorded by the careful observers who have written on this subject. When a snake is coiled flat, no muscular effort is necessary to hold that position. When the snake is coiled somewhat in a cone shape around its eggs, one can conceive that a certain amount of tension would be necessary to hold the conical form. That there is any great amount of tension is, however, greatly to be doubted. The importance of a further study of the incubating python became apparent upon reading the literature on this subject, and fortun-



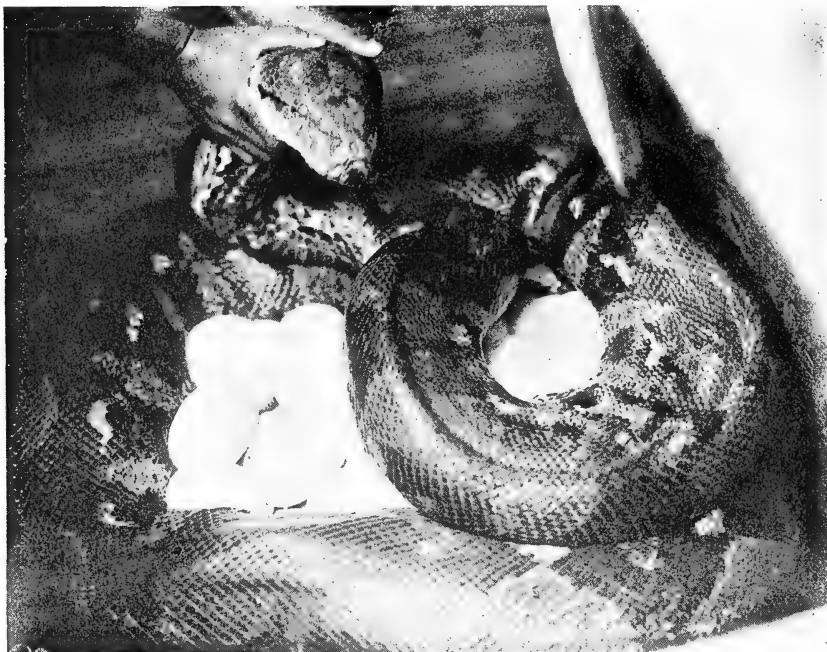


FIG. 22—PHOTOGRAPH OF AN 8-METER INCUBATING PYTHON.

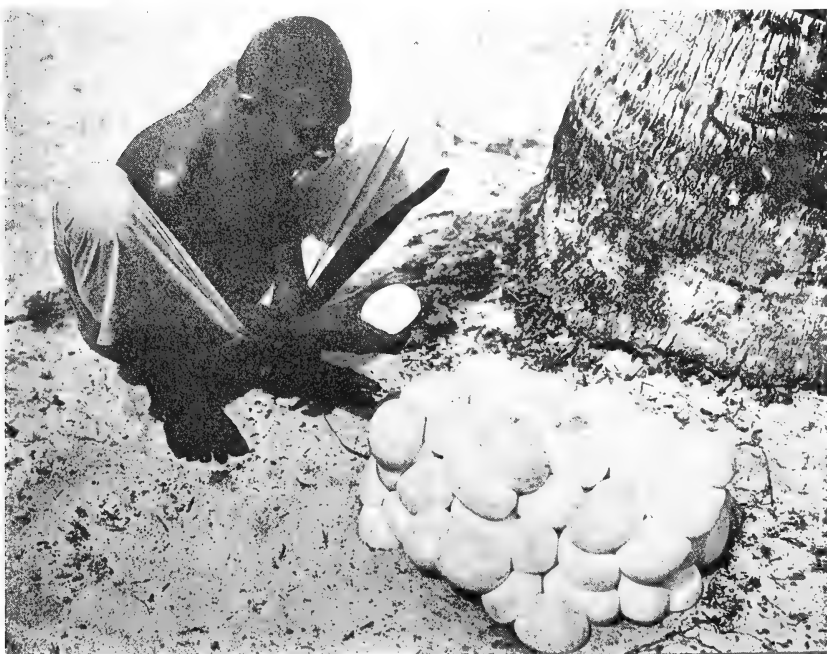


FIG. 23—EGGS LAID BY A PYTHON.

Photographs taken by Field Museum of Natural History on upper Ogan River in Sumatra, in 1929.

ately before this report was sent to the press, an opportunity was had to make some observations on such a snake.

On April 5, 1931, a python (*African sebæ*) laid approximately 20 eggs in the new reptile house of the National Zoological Park in Washington, D. C. The writer was given an opportunity to observe this animal, and arrangements were immediately made with Dr. William M. Mann, the Director of the Park, to undertake a careful survey of the environmental temperature and the body temperature of the python. In figure 24 is reproduced a photograph of this snake, which was originally published in the public press, unfortunately considerably altered for display purposes. Figure 24 shows the snake coiled around her eggs, apparently on the day on which they were laid. The efforts of the artist to touch up the original photograph have resulted in the head of the serpent appearing to have a rather grotesque form. This python had been brought to the National Zoological Park in 1927. At that time it was about 3.5 meters long, but had grown nearly a meter since its capture. On May 1, 1931, E. L. Fox of the Nutrition Laboratory staff, who has contributed so much to the study of snakes reported in this book, and our physicist, V. Coropatchinsky, went to Washington with instruments and made a careful temperature survey of the snake. At that time another photograph (fig. 25) was taken of the python coiled about her eggs. This shows the state of the eggs on May 1. At this time they had more or less the nature of dough. The lines of demarkation of the individual eggs were not always clear. (See observations of Dr. W. M. Mann, this report, page 113.) This is in striking contrast to the condition of the eggs shown in figure 24, which was taken on the day the eggs were laid.

In the den there were three pythons. On the night of April 5 the female python, which had not eaten for ten weeks, selected the extreme corner of the cage near the glass window, in front and at one side, there laid her eggs, and coiled about them. It was noted by the keepers that whereas formerly all three snakes had traveled about the cage at will, exploring nearly every corner of it, and were not inclined to stay in any one place more than any other, on this particular day both of the other snakes in their voyage around the cage crawled over the female and then went off immediately to the diagonally opposite end of the cage and had hardly left that corner since that day, at least not when observers were about. The female, therefore, remained entirely unmolested, right next to the glass window and hence in a good position for public view. A photograph of the python den in the National Zoological Park is shown in figure 26. At the extreme right, next to the glass window, is the incubating python coiled about her eggs. At the extreme left, at two different levels, are the other two pythons. These pythons remained in this part of the den for the greater part of the time. Only once during the day when our temperature studies were made did one of them stretch out to nearly its full length, but then immediately withdrew to its corner where it remained for the rest of the day.

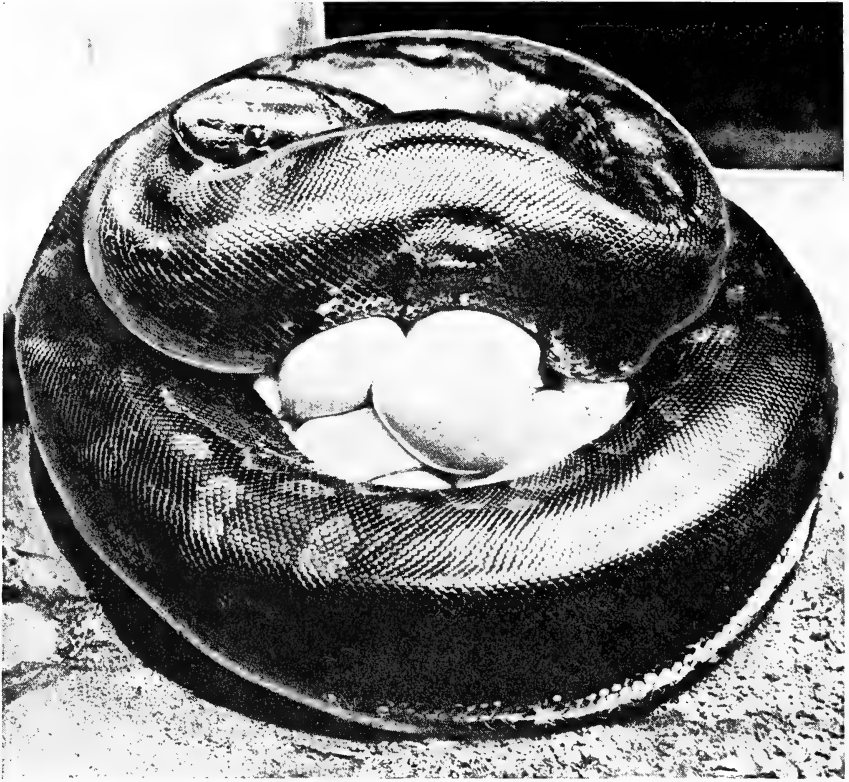


FIG. 24—PHOTOGRAPH OF AN INCUBATING PYTHON AT NATIONAL ZOOLOGICAL PARK IN WASHINGTON, D. C.

Photograph taken within a few hours after eggs were laid.

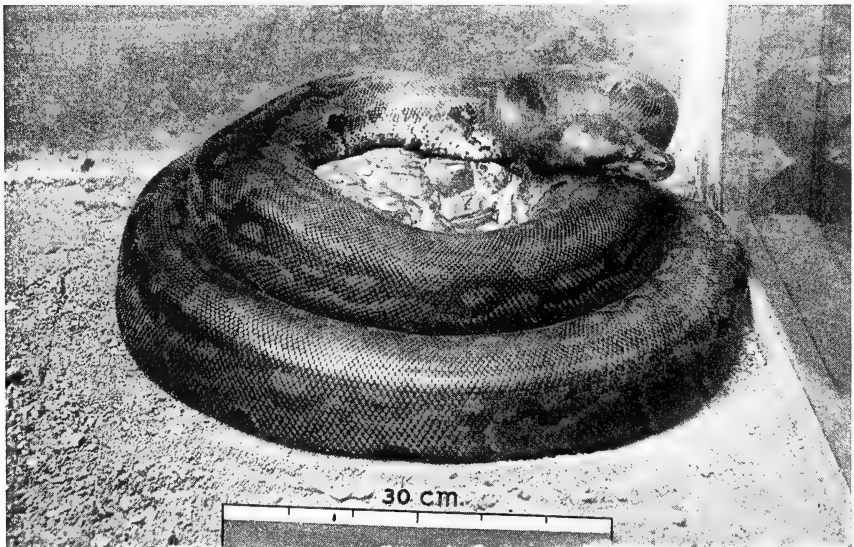


FIG. 25—PHOTOGRAPH OF AN INCUBATING PYTHON AT NATIONAL ZOOLOGICAL PARK IN WASHINGTON, D. C.

Photograph taken May 1, 1931, nearly one month after eggs were laid; shows dough-like nature of egg mass at that time.

The method of Selater and Forbes of making a comparative study of the temperature of the male and female would have been of no value in our survey. If the male could have been transported to the same corner where the female was, even then undoubtedly the agitation and disturbance of the male would have defeated our ends. As it was, rather considerable differences in temperature existed in the different parts of the cage throughout the day when our observations were made, although fortunately in the corner where the female was located the minimum variations in environmental temperature occurred.

The female python was reported as being unusually placid and quiet, had been many years in the park, had been frequently handled, and therefore was ideally adapted for this type of temperature study. Agitation or viciousness would have complicated the situation greatly, by causing of itself a rise in body temperature. Fortunately this complication was not encountered. Throughout the entire day on May 1, when Fox and Coropatchinsky were making their observations upon her, together with the extremely efficient caretaker, Mr. F. O. Lowe (without whose assistance we could have done little), the python only once indicated the slightest bit of disturbance. At one time in the afternoon when she was gently pushed to one side to give a view of the eggs, she hissed. In planning these temperature observations on the incubating python, we recognized that equal stress must be laid upon an accurate survey of the temperature of the environment. Obviously it would have been ideal to have recorded the rectal temperature. We did not dare to disturb the animal to take the rectal temperature, fearing she might permanently leave the eggs and thus precipitate a distinct calamity for a zoological park. As the result of our experience with this animal, however, and judging from the comments of Colonel Abbott in 1838 (see this report, page 90), we believe that the snake would have endured without too much agitation a great deal more handling than we dared to give her. Since it was realized that agitation would defeat our ends, every concession was made to approach the animal as quietly as possible and to avoid undue discomfort.

#### RESPIRATION RATE

To aid in determining whether the python was agitated between observations, it was planned to record for comparison her respiration rate before the operators entered the den and again two or three times during the day. It was reasoned that if the animal had been obviously disturbed or agitated between temperature surveys, this agitation would be reflected in the respiration rate. The records obtained of the respiration rate are given in tables 16 and 17. The respirations were somewhat irregular but usually were well marked, deep respirations with occasionally minor, small movements. The respirations were counted by E. L. Fox, who used a watch reading to decimal parts of a minute. The time on the watch was recorded at the end of each complete respiration. During the first series of observations from 10<sup>h</sup>30<sup>m</sup> to 10<sup>h</sup>50<sup>m</sup> a.m., 18 counts were made.



FIG. 26—SNAKE DEN AT NATIONAL ZOOLOGICAL PARK IN WASHINGTON, D. C.

Incubating python is near window, in front, right-hand corner. Other two snakes are at extreme left.

The average rate was 2.0 respirations per minute. Another series of 12 counts at about 11 a.m. showed an average rate of 2.3 respirations per minute. The sixth count in each of these series was omitted. The observations taken at 10<sup>h</sup>30<sup>m</sup> and 11 a.m. preceded any measurements of the temperature of the snake. The skin temperature survey began at 11<sup>h</sup>13<sup>m</sup> a.m. and continued throughout the afternoon with the observers working in the cage and sometimes almost over the snake, as will be seen in figure

TABLE 16—*Respiration rate of an incubating python*

10 <sup>h</sup> 30 <sup>m</sup> –10 <sup>h</sup> 50 <sup>m</sup> a.m.			11 <sup>h</sup> 00 <sup>m</sup> –11 <sup>h</sup> 06 <sup>m</sup> a.m.			1 <sup>h</sup> 47 <sup>m</sup> –1 <sup>h</sup> 52 <sup>m</sup> p.m.		
Number of respira- tions	Time on watch	Rate per minute	Number of respira- tions	Time on watch	Rate per minute	Number of respira- tions	Time on watch	Rate per minute
	<i>min.</i>			<i>min.</i>			<i>min.</i>	
10	4.11	2.4	1	0.52	1.9	1	0.51	2.0
7	3.02	2.3	2	0.76	2.6	2	0.91	2.2
1	0.42	2.4	3	1.15	2.6	3	1.23	2.4
2	1.00	2.0	4	1.36	2.9	4	1.52	2.6
3	1.52	2.0	5	2.00	2.5	5	2.91	1.7
4	2.21	1.8	6	....	...	6	3.24	1.8
5	2.79	1.8	7	3.12	2.2	7	3.60	1.9
6	....	...	8	3.52	2.3	8	4.11	1.9
7	3.70	1.9	9	4.11	2.2	9	4.40	2.0
8	4.28	1.9	10	4.39	2.3	10	4.92	2.0
9	4.88	1.8	11	4.92	2.2	11	5.16	2.1
10	5.20	1.9	12	5.62	2.1	..	....	...
11	5.65	1.9	..	....	...	..	....	...
12	5.93	2.0	..	....	...	..	....	...
13	6.46	2.0	..	....	...	..	....	...
14	6.75	2.1	..	....	...	..	....	...
15	7.50	2.0	..	....	...	..	....	...
16	....	...	..	....	...	..	....	...
17	8.70	1.9	..	....	...	..	....	...
18	9.50	1.9	..	....	...	..	....	...
Avg.		2.0			2.3			2.0

27, page 102. Between 1<sup>h</sup>47<sup>m</sup> and 1<sup>h</sup>52<sup>m</sup> p.m., at the end of the morning's temperature observations, 11 respirations were counted and the average rate was 2.0 per minute, an insignificant change from the first two series in the morning. At 3<sup>h</sup>13<sup>m</sup> p.m., when the operators returned from an hour's absence for lunch, 14 counts showed an average rate of 2.2 respirations per minute. At 3<sup>h</sup>34<sup>m</sup> p.m. another series of 15 counts showed a distinctly faster rate, averaging 3.1 per minute. Although probably without significance the keeper, Mr. Lowe, opened the cage door and sat in the doorway just prior to this particular set of readings. Two temperature surveys were then made throughout the afternoon, during which time the python was almost continually handled and touched either with the thermo-junction or, at times, by the hand with rarely an indication of irritation. Between 5<sup>h</sup>15<sup>m</sup> p.m. and 5<sup>h</sup>26<sup>m</sup> p.m., 30 counts showed an average rate of 3.0 respirations per minute. This rate was slightly higher

than that of the morning, but can hardly be taken as indicating any significant amount of agitation and certainly not an agitation of the order we found necessary to raise materially the snake's temperature in our New York studies. This respiration study confirms our belief that with this particular python the temperatures measured were unaffected by any agitation. The last series of counts in the afternoon, which showed a

TABLE 17—*Respiration rate of an incubating python*

3 <sup>h</sup> 13 <sup>m</sup> –3 <sup>h</sup> 27 <sup>m</sup> p.m.			3 <sup>h</sup> 34 <sup>m</sup> –3 <sup>h</sup> 40 <sup>m</sup> p.m.			5 <sup>h</sup> 15 <sup>m</sup> –5 <sup>h</sup> 26 <sup>m</sup> p.m.		
Number of respirations	Time on watch	Rate per minute	Number of respirations	Time on watch	Rate per minute	Number of respirations	Time on watch	Rate per minute
	<i>min.</i>			<i>min.</i>			<i>min.</i>	
1	0.40	2.5	1	0.22	4.5	1	0.21	4.8
1	0.52	1.9	2	0.53	3.8	2	0.61	3.3
2	0.81	2.5	3	0.80	3.7	3	0.82	3.7
3	1.60	1.9	4	1.13	3.5	4	1.39	2.9
4	2.30	1.7	5	1.48	3.4	5	1.81	2.8
5	2.56	1.9	6	2.03	3.0	6	2.12	2.8
6	2.81	2.1	7	2.48	2.8	7	2.41	2.9
7	3.02	2.3	8	2.80	2.9	8	2.77	2.9
8	3.63	2.2	9	3.31	2.7	9	3.04	3.0
9	3.84	2.3	10	3.60	2.8	10	3.57	2.8
10	4.13	2.4	11	4.02	2.7	11	3.93	2.8
11	4.58	2.4	12	4.31	2.8	12	....	...
12	5.11	2.3	13	4.84	2.7	13	4.71	2.8
13	5.66	2.3	14	5.23	2.7	14	4.92	2.8
14	5.95	2.3	15	5.54	2.7	15	5.24	2.9
..	....	...	..	....	...	16	5.25	3.0
..	....	...	..	....	...	17	6.07	2.8
..	....	...	..	....	...	18	6.30	2.9
..	....	...	..	....	...	19	6.67	2.8
..	....	...	..	....	...	20	6.92	2.9
..	....	...	..	....	...	21	7.70	2.7
..	....	...	..	....	...	22	7.91	2.8
..	....	...	..	....	...	23	8.11	2.8
..	....	...	..	....	...	24	8.31	2.9
..	....	...	..	....	...	25	8.92	2.8
..	....	...	..	....	...	26	9.13	2.8
..	....	...	..	....	...	27	9.62	2.8
..	....	...	..	....	...	28	10.10	2.8
..	....	...	..	....	...	29	10.39	2.8
..	....	...	..	....	...	30	10.92	2.7
Avg.		2.2			3.1			3.0

slightly higher respiration rate, were coincidental with a slightly higher body temperature, as will be seen by further consideration of the data.

In our study of the respiration rate of snakes in the New York Zoological Park it was found that the average respiration rate was 2.1 per minute (see page 51) or not far from the average rate (2.5) of this incubating python. The temperature of the incubating python was, however, probably 3° or 4° higher than that of the snakes studied in New York, a fact which might of itself account for the slight difference in the respiration

rate in the two series. It might be argued that with a respiration rate as low as 2.5 there could not have been any great increase in metabolism, and a more rapid respiration rate might have been necessary to enable the elimination of the carbon dioxide produced. The snakes whose respiration rates were observed in New York were much larger than this incubating python, 6- or 7-meter pythons as compared with the 5-meter incubating python, and the respiration rate itself is not necessarily an index of the volume of respiration. Hence any inference with regard to the total metabolism from the respiration rate is not justifiable.

#### METHODS OF OBTAINING TEMPERATURE MEASUREMENTS

In the well-planned reptile house in the Zoological Park at Washington it was feasible to set up all the apparatus in back of the cages in a satisfactory, well-lighted place. On this particular day the environmental temperature was very high for human comfort, and one had to be extremely careful not to have undue movements of air inside the snake's cage. The operator, Fox, and the keeper, Lowe, spent a good part of the day in the den with the python and found it very warm. The sky-lights in the reptile house were provided with a glass having a high transmission of ultra-violet rays. Considerable sunlight thus came into the snake chamber, and this aided in developing a rather high temperature, although the sun at no time came in contact with the brooding python. The hot-water pipes under the gravel floor were used only in the coldest weather and had not been used for some time. The chamber was heated, when necessary, by a series of hot-water coils, fastened to the walls just above the long plate-glass window of the den, at a fairly high level.

After the first two series of respiration counts were made in the morning by noting the respirations through the glass, the observers entered the den and made a complete survey of the temperature of the air about the python, of the temperature of the gravel, of the temperature between the folds of the snake, and of the temperature on the surface of the snake at different points. It was believed that only with this complete program could a definite conclusion be drawn. Certainly the temperature measurements of the animal itself are without significance unless the temperature of the environment is accurately known. A thermometer hung in the cage is without value if the air is stratified, and the stratification depends in large part upon the local heating. It was emphasized to the observers that a temperature survey of the air was equally as important as any survey of the temperature on the surface or between the folds of the animal. At the end of the forenoon's work the operators withdrew from the cage for an hour. During this time the apparatus was practically dismantled and the temperature of the thermostat was purposely somewhat altered so that, on the return of the operators to the cage in the afternoon, the observations would represent practically a new survey, since it would be necessary to reassemble the apparatus and calibrate the thermo-junction. Two complete temperature surveys were made in the afternoon. Hence three series of measurements are available for comparison, in which the temperature of the environmental air was most elaborately studied.



The techniques employed were almost entirely thermo-electric. For the skin-temperature measurements, the apparatus described by Benedict, Coropatchinsky, and Finn was used,<sup>1</sup> with two methods of application of the junction. In some instances the application junction was protected



FIG. 27—MEASUREMENT OF SKIN TEMPERATURE OF AN INCUBATING PYTHON BY E. L. FOX AT NATIONAL ZOOLOGICAL PARK IN WASHINGTON, D. C.

Application junction laid on surface of snake, unprotected by hard-rubber backing. Electrically controlled thermostat in center of picture near snake.

with a standard hard rubber backing and cotton batting and was applied to the skin of the snake much as it is applied in the case of humans. This protection was always used when the junction was laid on the surface of the snake. In other instances, especially when taking the skin temperature between the folds, the junction was not protected by the rubber backing but was applied directly to the skin, as shown in figure 27.<sup>2</sup> From the calibration of the apparatus, from the deflection of the galvanometer at the time the junction was applied to the skin, and from the temperature of the thermostat the true skin temperature could be computed. The protection of the application junction by a backing has been called in ques-

<sup>1</sup> Benedict, F. G., V. Coropatchinsky, and M. D. Finn, Journ. de Physiol. et de Path. gén., 1928, **26**, p. 1; *ibid.*, Leopoldina (Amerikaband), Berichte d. Kaiserl. Leopold. Deutsch. Akad. d. Naturforscher, Halle, 1929, **4**, p. 129.

<sup>2</sup> This photograph was taken by Underwood and Underwood.

tion by Aldrich.<sup>1</sup> To answer this possible criticism, the backing on the application junction was removed and a series of observations made with the bare junction. The bare junction was especially desirable in determining the temperature between the folds of the snake, for it could easily be directly inserted between the folds without disturbing the snake. When the junction was inserted between the folds, the snake usually separated the two coils slightly, allowing the junction to enter freely, and then almost immediately the snake settled back so that the junction was held firmly in contact with the two coils.

The measurements of the air temperature were made in two ways. One end of the standard skin-temperature thermo-junction was placed in a thermostat, the temperature of which was exactly known. From the readings on the galvanometer, which had previously been calibrated, one could compute exactly the temperature of the other junction, which was held in the air. For further insurance against possibility of error, a second survey of the air temperature was made with a differential thermo-junction. A fork was fashioned from a 60-cm. length of constantan wire, soldered to two copper leads connecting with the galvanometer. One end of the fork was placed on the snake or in the gravel at any desired spot, and the other end, 60 cm. away, was held in the air in a horizontal position to allow for any possible differences in the stratification of the air. This latter junction was provided with a sensitive mercurial thermometer that could be read directly. The differential reading between the two junctions was noted on the galvanometer. By this means a survey of the temperature of the air and the temperature of the gravel or of the snake could be made and checked with the direct junction method. In all cases a most satisfactory agreement was found. A small, portable, electrically controlled thermostat and heater (see figure 27) were especially constructed by Mr. Coropatchinsky to hold automatically the constant temperature junction at approximately 30° to 32°.

#### TEMPERATURE MEASUREMENTS

The earlier studies in the literature and our own experience at the New York Zoological Park and at the Nutrition Laboratory in Boston have stressed the difficulties of determining the true environmental temperature. Since the snake den in the Zoological Park in Washington was large and the incubating python was located in one corner, near a glass window that was but a few centimeters from the cold air in the corridor outside, it was feared that the temperature of the environment here would be far from constant. A thermometer hung in the den at about the level of one of the trees showed a variation throughout the afternoon of from 33° to 29° C. Just what would be the air currents in the corner of the den where the incubating python was lying could not be predicted. The opening of the door for the operators to enter and leave might of itself produce air currents. The first determinations therefore represented a de-

<sup>1</sup> Aldrich, L. B., *A Study of Body Radiation*, Smithsonian Misc. Collections, 1928, **81**, No. 6, p. 10.

tailed survey of the temperature of the air about the snake and the temperature of the gravel, compared with the temperatures on the surface and between the folds of the snake. The results of this first survey, which

TABLE 18—*Comparison of environmental temperature with the skin temperature of an incubating python (11<sup>h</sup>13<sup>m</sup> a.m. to 12<sup>h</sup>25<sup>m</sup> p.m.)*

Environmental temperature				Skin temperature				
On gravel around python	10 to 15 cm. above floor	30 cm. above floor	60 cm. above floor	Under python	On surface			Between folds
					Near gravel	Covered junction	Uncovered junction	
°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.
31.72	32.00	31.12	31.32	33.20	33.01	34.21	33.76	33.68
31.51	31.11	31.64	31.24	34.03	33.25	34.29	33.21	33.82
31.30	31.70	31.96	31.12	32.74	32.85	33.89	33.58	33.33
31.34	31.69	31.12	31.44	32.78	32.98	33.53	33.49	33.80
31.38	31.60	31.08	31.32	32.72	33.30	35.33	33.38	33.81
31.74	30.92	31.20	31.20	32.72	32.62	34.09	.....	33.77
31.52	31.00	31.12	31.36	33.34	.....	34.25	.....	33.57
30.57	30.80	31.04	31.00	33.14	.....	33.97	.....	34.21
31.54	30.92	31.04	31.16	32.58	.....	34.01	.....	33.89
31.62	31.76	31.04	.....	34.22	.....	33.69	.....	33.97
31.54	31.04	29.82	.....	.....	.....	33.73	.....	33.90
31.38	30.84	29.82	.....	.....	.....	33.41	.....	33.98
31.20	30.84	30.02	.....	.....	.....	33.25	.....	33.58
31.60	32.04	30.06	.....	.....	.....	33.73	.....	34.14
31.80	30.84	30.33	.....	.....	.....	33.09	.....	34.30
30.36	30.84	32.00	.....	.....	.....	33.61	.....	.....
32.44	31.32	32.02	.....	.....	.....	33.85	.....	.....
32.16	29.80	31.91	.....	.....	.....	33.66	.....	.....
31.72	29.52	31.94	.....	.....	.....	33.90	.....	.....
31.56	29.56	.....	.....	.....	.....	33.58	.....	.....
31.24	.....	.....	.....	.....	.....	32.98	.....	.....
31.32	.....	.....	.....	.....	.....	33.82	.....	.....
32.04	.....	.....	.....	.....	.....	33.46	.....	.....
31.04	.....	.....	.....	.....	.....	33.86	.....	.....
30.48	.....	.....	.....	.....	.....	33.74	.....	.....
29.92	.....	.....	.....	.....	.....	33.90	.....	.....
31.38	.....	.....	.....	.....	.....	34.02	.....	.....
.....	.....	.....	.....	.....	.....	32.86	.....	.....
.....	.....	.....	.....	.....	.....	33.22	.....	.....
.....	.....	.....	.....	.....	.....	33.74	.....	.....
.....	.....	.....	.....	.....	.....	33.38	.....	.....
.....	.....	.....	.....	.....	.....	33.62	.....	.....
.....	.....	.....	.....	.....	.....	33.62	.....	.....
Avg. 31.38	31.01	31.07	31.24	33.15	33.00	33.73	33.48	33.85

was completed at 12<sup>h</sup>25<sup>m</sup> p.m., are shown in table 18. It was assumed that the snake in a cubical box of air (60 by 60 by 60 cm.) and measurements of the temperature of the air in this hypothetical box were taken at the corners and at different points away from the snake, on the sides, and to a height of 60 cm. above the floor. The observations in table 18 are recorded without regard to the exact location of the air temperatures.

The gravel around the python had an average temperature of  $31.38^{\circ}\text{C}$ . The temperature of the air 10 to 15 cm. above the gravel averaged  $31.01^{\circ}$ ; 30 cm. above it averaged  $31.07^{\circ}$  and 60 cm. above,  $31.24^{\circ}\text{C}$ . The temperature between the python and the gravel averaged  $33.15^{\circ}$ . Six observations on the side of the snake approaching the belly and near the gravel gave an average of  $33.00^{\circ}$ . The temperature on the surface of the snake was determined with the thermo-junction protected with the hard-rubber backing (fig. 28). Thirty-three observations gave an average surface temperature of  $33.73^{\circ}$ . Five observations on the skin with the junction uncovered showed an average temperature of  $33.48^{\circ}$ , and 15 observations between the folds,  $33.85^{\circ}$ . These average values indicate that in general the temperature of the environment was  $31.2^{\circ}$ , the temperature on the skin of the snake  $33.5^{\circ}$ , and the temperature between the folds of the snake  $33.85^{\circ}$ . These measurements clearly establish the fact that there was a difference in temperature between the snake and the environment of, on the average,  $2.5^{\circ}\text{C}$ .

One of the surprising features of this particular survey was the general uniformity of the temperature of the air in this corner of the python den at the different levels at which the measurements were made, the highest level in this case being 60 cm. from the floor. To aid in visualizing the exact location of the various temperature measurements that were made in this first series, representative values have been written directly on photographs of the snake. Thus, in figure 29 the upper photograph shows the location of some (not all) of the air temperatures taken between  $11^{\text{h}}13^{\text{m}}$  and  $11^{\text{h}}57^{\text{m}}$  a.m., and the lower photograph shows temperatures on the surface and between the folds of the snake taken during the same time. The arrows indicate temperatures between the folds of the snake. The small dots near the temperature values show the exact location of the temperature measurements on the surface of the snake or in the air. The temperatures marked by crosses were taken in the air 30 cm. above the floor. The ruler on the floor serves to show the dimensions of the snake and likewise the approximate dimensions of the imaginary air box. In figure 30 another typical series of readings is shown, taken at  $12^{\text{h}}25^{\text{m}}$  p.m. Here again the upper photograph gives the air temperatures and the lower the snake temperatures.

Between  $3^{\text{h}}40^{\text{m}}$  p.m. and  $4^{\text{h}}05^{\text{m}}$  p.m. a second survey was made. At this time it was becoming cloudy. There was no sun and there were changes in the temperature of the air in the den. Although the morning series had established clearly that there was no appreciable gradient in air temperature and practically no air movement, it would perhaps have been of value to have determined by means of the smoke from a burning cigarette or joss stick the presence or absence of air currents and their relation to the window, the wall, and the center of the cage. In any event, such air currents must have been very feeble. The temperatures of the wet and the dry bulb thermometers were not recorded, and hence the humidity existing at the time of the different surveys is not known. The air in the den, although warm and uncomfortable, was probably not saturated. The temperature of the air in the outside corridor was  $20.4^{\circ}$

and the inside of the glass window in the den must have been below the temperature of the air in the den, because cooled by the temperature of the corridor air. Hence if the air inside the den had been saturated, there would have been condensation on the window, which was not the case. A probable figure for the degree of humidity would be approximately 80 per cent saturation at 31° C.



FIG. 28—MEASUREMENT OF SKIN TEMPERATURE OF AN INCUBATING PYTHON AT NATIONAL ZOOLOGICAL PARK IN WASHINGTON, D. C.

Application junction, protected with hard-rubber backing, is shown resting on snake. Electrically controlled thermostat and heater at left, in rear of snake.

In the survey made at about 4 p.m. it was assumed that the snake was in a triangular air box, and the air temperatures accordingly were taken at different levels in the three corners of this imaginary triangle to a height of 60 cm. A complete list of these observations is given in table 19 and typical readings to show the location of the measurements are given in figure 31. There was no evidence of any appreciable stratification of the air. The gravel unaccountably had a temperature somewhat above that of the air. We were assured that the heating system had been out of commission for some time. The source of this heat is difficult to understand, unless possibly it was derived from the body of the snake. Yet the poor conductivity of the gravel would hardly lead one to expect such a rise in temperature, although the gravel temperatures were taken but 5 cm. from the point of contact between the snake and the gravel.

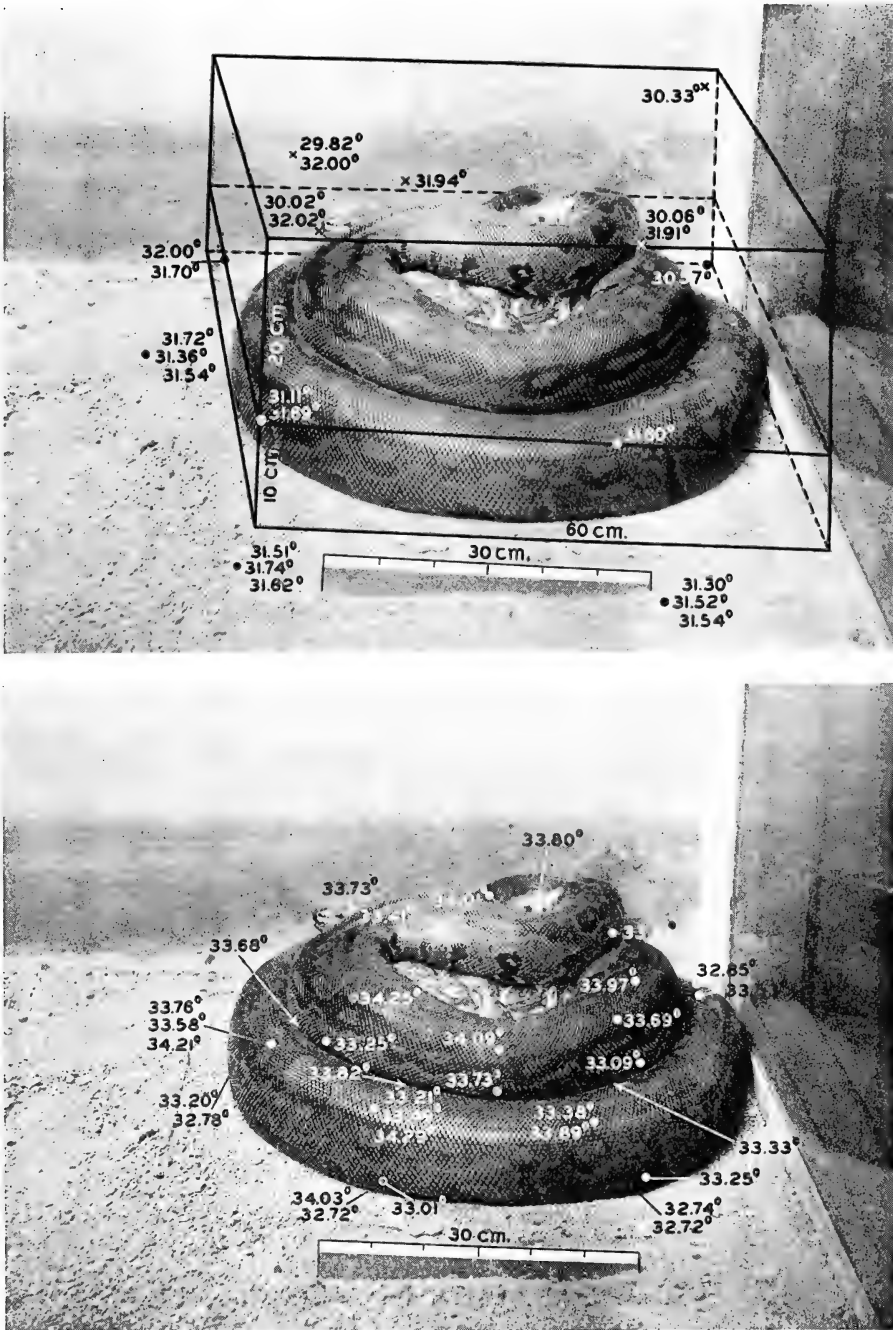


FIG. 29—COMPARISON OF SKIN TEMPERATURE OF AN INCUBATING PYTHON WITH ITS ENVIRONMENTAL TEMPERATURE.

Observations were taken between 11<sup>h</sup>13<sup>m</sup> and 11<sup>h</sup>57<sup>m</sup> A.M. Upper photograph shows location of temperature measurements of air about snake. Lower photograph shows temperatures on surface and between folds of snake, determined at same time as environmental temperature. Arrows indicate temperatures between folds. Small solid dots show exact location of temperature measurements on surface of snake or in air. Air temperatures marked with crosses were 30 cm. above floor.

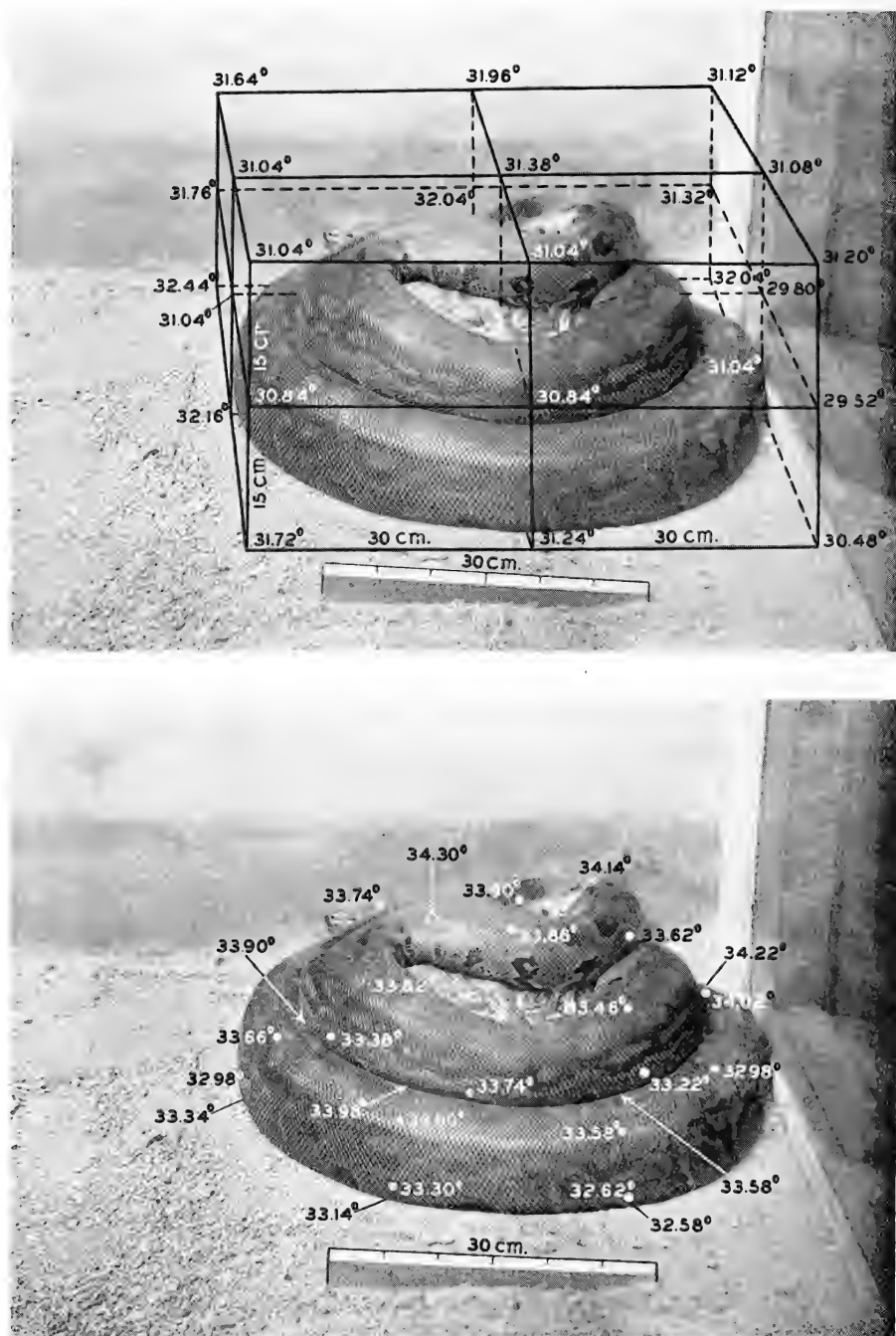


FIG. 30—COMPARISON OF SKIN TEMPERATURE OF AN INCUBATING PYTHON WITH ITS ENVIRONMENTAL TEMPERATURE.

Observations were taken at 12<sup>h</sup>25<sup>m</sup> P.M. Upper photograph shows location of measurements of air temperature and lower photograph temperatures on surface and between folds of snake. Arrows indicate temperatures between folds. Small solid dots show exact location of temperature measurements.

Farther from the snake the gravel temperature was usually  $1.5^{\circ}$  to  $2^{\circ}$  lower. It is significant that the air 10 to 15 cm. above the gravel has a temperature averaging somewhat over  $2^{\circ}$  lower than that of the gravel. The air 30 and 60 cm. above the floor had an essentially constant temperature of not far from  $30^{\circ}$ . In the rear corner of the imaginary triangular air box, that is, the corner nearest the glass window and the wall, the air temperatures were about  $0.8^{\circ}$  or  $0.9^{\circ}$  above those in the middle foreground. One would have expected the reverse, since the temperatures

TABLE 19—*Comparison of environmental temperature with skin temperature of an incubating python (3<sup>h</sup>40<sup>m</sup> to 4<sup>h</sup>05<sup>m</sup> p.m.)*

Environmental temperature				Skin temperature		
On gravel around python	10 to 15 cm. above floor	30 cm. above floor	60 cm. above floor	Under python	On surface (covered junction)	Between folds
$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$	$^{\circ}\text{C.}$
32.32	29.96	30.55	29.92	33.39	33.85	34.27
32.34	29.34	30.50	30.46	33.64	35.26	34.42
32.82	30.98	30.38	30.94	33.24	35.06	34.15
.....	30.32	30.35	.....	33.37	34.30	34.16
.....	29.46	30.32	.....	32.42	34.50	33.91
.....	30.98	30.32	.....	32.38	34.06	34.82
.....	30.50	29.90	.....	32.94	34.10	35.10
.....	30.29	30.78	.....	33.82	34.34	35.06
.....	.....	.....	.....	33.74	33.98	34.98
.....	.....	.....	.....	33.74	34.18	35.18
.....	.....	.....	.....	33.43	34.74	.....
.....	.....	.....	.....	33.14	33.86	.....
.....	.....	.....	.....	33.91	33.94	.....
.....	.....	.....	.....	34.62	34.06	.....
.....	.....	.....	.....	32.07	34.34	.....
.....	.....	.....	.....	.....	34.34	.....
Avg. 32.49	30.23	30.39	30.44	33.32	34.31	34.61

in the rear were taken near the glass, which was affected by the cold air of the outside corridor. In any event, it is clear that the temperature of the environment of the snake in this particular series was well established and was not far from  $30.4^{\circ}$ , on the average. The temperatures of the snake itself, both on the skin and between the folds, were as high as  $35.06^{\circ}$ ,  $35.10^{\circ}$ ,  $35.18^{\circ}$  and  $35.26^{\circ}$ , and practically all of them were above  $34^{\circ}$ . There was, therefore, at this time a difference of at least  $4^{\circ}$  C. between the air temperature and the temperature of the snake. The average temperature of the snake in this four o'clock series,  $34^{\circ}$ , was a little higher than the average body temperatures in the morning series, namely,  $33.5^{\circ}$  to  $33.85^{\circ}$ , in spite of the fact that the environmental temperature was nearly one degree below that in the morning. Whether this is of real significance or whether it simply means that there was a small amount of agitation, although hardly detectable, on the part of the snake, can not be



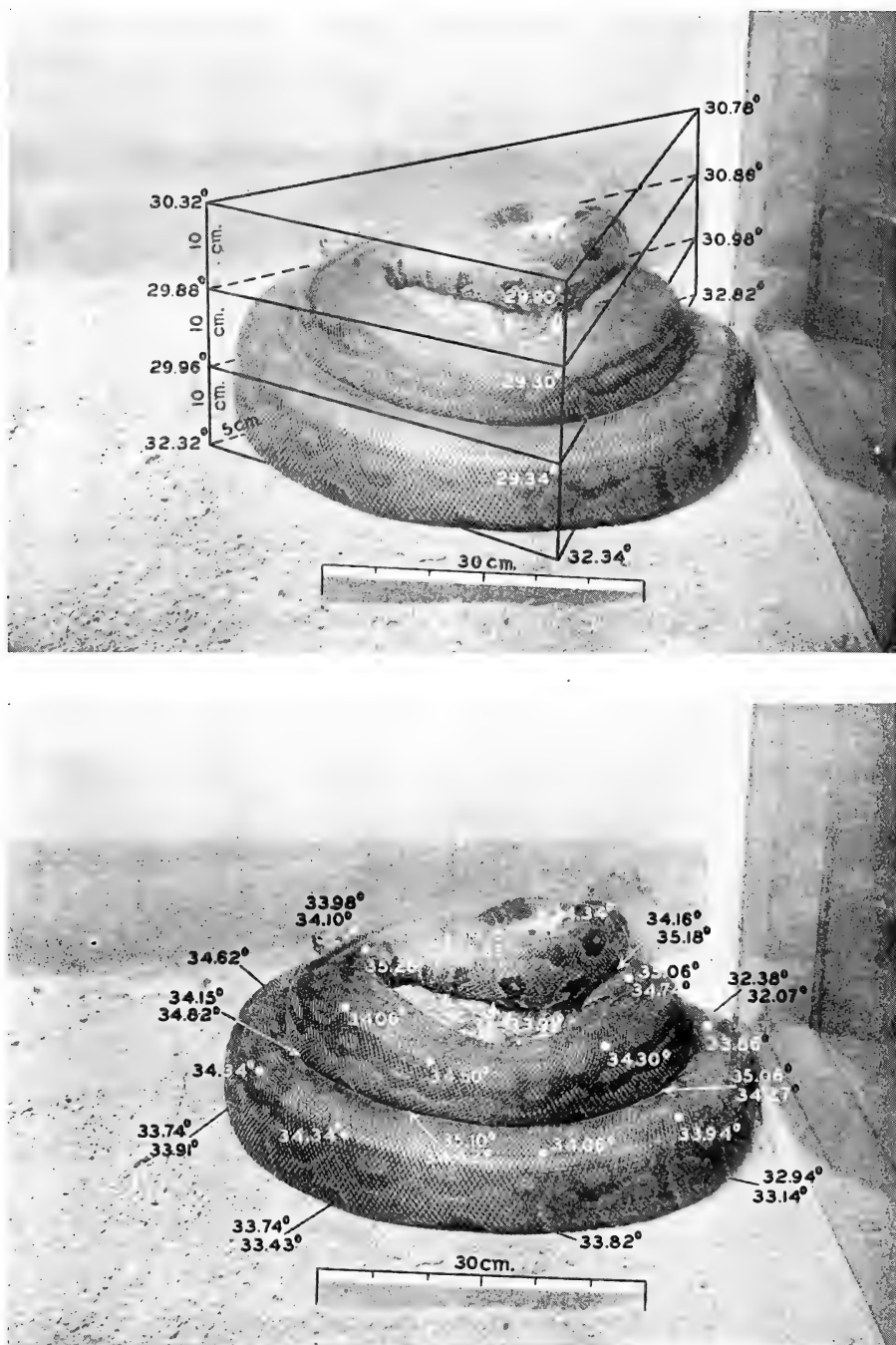


FIG. 31—COMPARISON OF SKIN TEMPERATURE OF AN INCUBATING PYTHON WITH ITS ENVIRONMENTAL TEMPERATURE.

Air temperatures shown in upper photograph were taken at 4<sup>h</sup>10<sup>m</sup> P.M. Skin temperatures shown in lower photograph were taken between 3<sup>h</sup>45<sup>m</sup> and 4<sup>h</sup>10<sup>m</sup> P.M. Arrows indicate temperatures between folds of snake. Small solid dots show exact location of temperature measurements.

determined, but certainly a temperature potential of approximately 4° was shown in the four o'clock series.

Between 4 and 5 p.m. the third and last survey was made. Again the snake was assumed to be in a triangular-shaped air box and the measurements were made accordingly. The results are recorded in table 20 and a typical illustration is given in figure 32. The gravel near the snake was warm, possibly from the body of the snake. The average environmental

TABLE 20—Comparison of environmental temperature with skin temperature of an incubating python (4<sup>h</sup>05<sup>m</sup> to 5<sup>h</sup>15<sup>m</sup> p.m.)

Environmental temperature				Skin temperature			
On gravel around python	10 to 15 cm. above floor	30 cm. above floor	60 cm. above floor	Under python	On surface		Between folds
					Near gravel	Covered junction <sup>1</sup>	
°C.	°C.	°C.	°C.	°C.	°C.	°C.	°C.
30.19	31.77	29.44	29.16	32.07	33.45	33.73	34.79
30.74	31.49	29.32	29.40	33.14	33.17	33.45	35.01
30.63	31.56	29.59	29.43	33.43	33.29	33.73	35.06
31.19	31.04	29.30	29.14	33.91	32.85	33.61	34.48
31.00	30.56	29.38	.....	34.62	.....	33.93	34.28
32.44	30.44	.....	.....	33.34	.....	34.09	34.22
31.44	29.84	.....	.....	33.30	.....	33.49	34.93
31.03	29.20	.. .	.....	33.34	.....	33.53	34.89
.....	30.11	.....	.....	32.94	.....	34.05	34.81
.....	.....	.....	.....	32.18	.....	33.97	34.77
.....	.....	.....	.....	.....	.....	33.69	35.13
.....	.....	.....	.....	.....	.....	34.49	35.01
.....	.....	.....	.....	.....	.....	34.17	35.17
.....	.....	.....	.....	.....	.....	34.57	.....
.....	.....	.....	.....	.....	.....	33.93	.....
.....	.....	.....	.....	.....	.....	33.93	.....
.....	.....	.....	.....	.....	.....	33.97	.....
Avg.31.08	30.67	29.41	29.28	33.23	33.19	33.90	34.81

<sup>1</sup>One reading with uncovered junction on the surface of snake showed a temperature of 32.34° C.

temperature 30 and 60 cm. above the snake was at this time not far from 29.5°, or measurably below that at about four o'clock. The temperature of the snake itself, on the other hand, both on the surface and between the folds, was almost the same as at four o'clock. Thus in about an hour's time there was a relatively small change in environmental temperature but the snake underwent no appreciable change in its body temperature. This is as is to be expected. This third series, like the second series, proves that there was a definite temperature potential between the snake and the environment of the order of 3° or 4° C. Furthermore, in those instances when the forked junction was used, one junction in the air and the other on the surface of the animal or between the folds of the



animal, the temperature gradient was strikingly uniform around the entire animal, corresponding to from  $3^{\circ}$  to  $3.5^{\circ}$  C.<sup>1</sup>

If it is assumed for the moment that the lower temperature potential of  $3^{\circ}$  prevailed, one could make a rough estimate as to the probable amount of heat lost in the form of sensible heat, although, since the emissivity of the snake's skin is not known, the heat lost from the surface of the skin can not be accurately calculated. This particular snake was 4.6 meters long or not far from the length (5 meters) of the 32-kg. python studied at the New York Zoological Park. This 32-kg. python was found by actual measurements of girths and length to have a surface area of 1.44 square meters, and this may be assumed to have been the surface area of the incubating python likewise. It is impossible to calculate accurately what proportion of this area was actually exposed to loss of heat by radiation, for undoubtedly the lower part of the snake's body resting on the gravel was well insulated, the part around the eggs was well insulated, and the radiation would be chiefly from the visible surface. If a rough estimate is made that this visible surface corresponded in the case of this incubating python to approximately two-thirds of the total surface, then the exposed surface would amount to 0.96 square meter and this exposed surface has a temperature potential of  $3^{\circ}$  C. Without making any speculative calculations, one can see that a considerable amount of sensible heat must have been lost by this animal to the environment. Indeed, a considerable amount of heat must have been produced to maintain this temperature potential of  $3^{\circ}$ , even if the emissivity is extremely small (which it is not likely to be), owing to the well-known tendency for vaporization of water from the body of the snake.

Theoretically a considerable amount of heat may have been developed by the putrefying eggs, but the heat from this source could not represent any considerable proportion of the total heat probably lost by the snake. Due to an oversight in planning this study of the incubating python, instructions were not given to measure the temperature of the egg mass. Since it is conceivable that the heat of the serpent might have been derived entirely from the putrefying eggs, such temperatures should have been taken. From an examination of figure 31 it can be seen that two records were secured of temperatures between the snake and the egg mass, both readings showing a temperature of  $33.91^{\circ}$ . If the eggs had been the *source* of heat, one would have found a higher temperature. But these two temperatures are slightly lower than the temperatures taken on the upper coils of the snake. Hence, one can infer that the eggs received heat from the snake rather than gave off heat to the snake.<sup>2</sup>

All the evidence, therefore, points clearly to an actual production of sensible heat by this incubating python, a large share of which, however,

<sup>1</sup>Under these conditions the temperature differential noted is really somewhat too small in all cases, for if the air junction had been shielded from the radiation from the snake, there would have been a somewhat lower air temperature.

<sup>2</sup>Dr. W. M. Mann writes that "on June 3, after having been coiled around the eggs since April 5, the python definitely left them. There were 20 eggs. Before they were sent to the Museum a few of them were opened and found to be full of paste, with no sign of an embryo." Although these eggs appeared to be a dough-like mass, they were easily separated and the relatively small amount of putrefaction that had taken place was not sufficient to disintegrate them.

does not contribute toward keeping the eggs warm but actually is lost to the environment. The mechanism for this heat production is not known. In all probability this condition of the incubating python corresponds to the febrile state shown by the higher order of animals, the birds, in incubating their eggs. Although this incubating python was slightly disturbed at times, the records of respiration rate indicate that she had a fairly placid disposition; hence the heat production undoubtedly did not result from agitation, but is unquestionably an internal process and the snake may possibly be considered to have been in a febrile state. One can now appreciate, even more fully than before, Krogh's<sup>1</sup> regret at being unable to make gaseous metabolism measurements on the incubating python.

Of special interest in connection with the attempts to compare the metabolism of cold-blooded animals with that of warm-blooded animals by bringing the cold-blooded animal to a high body temperature (see later discussion on pages 494 to 506) is the fact that this particular snake existed for many weeks at a body temperature measurably above 30°, having at times a temperature between the coils of close on to 34° or 35° C. It therefore seems unreasonable to suppose that, if the incubation process can result in maintaining a body temperature as high as this, the snake can undergo any appreciable damage when experimented upon at 37°.

The disposition of this particular type of snake to incubate its eggs is an astounding zoological trait. Since in the animal kingdom the birds represent the next highest stage in the development from the reptile, and since birds invariably incubate their eggs, it is possible that the incubating python represents one "milestone" (as Hall and Root<sup>2</sup> have so aptly expressed it) in the step from the cold-blooded or poikilotherm to the homoiotherm.

### WATER-VAPOR OUTPUT OF SNAKES

Under the head of respiratory exchange one usually considers only the elimination of carbon dioxide and the absorption of oxygen. The water vapor, as a rule, does not enter into such considerations, for measurement of the water vapor given off from the lungs alone (as is commonly the case in respiration experiments) would have no particular value unless accompanied by simultaneous measurement of the large amount lost from the skin. With these snakes, since invariably their respiratory exchange was studied in a closed-circuit chamber, it became feasible and in many cases desirable to measure the water vaporized. Hence the technique was at times adjusted to include direct determinations of the water vaporized as well as the carbon dioxide produced. To differentiate between the water vapor actually given off from the lungs and skin of an animal, that existing in the respiration chamber, and that arising from possible excretions (to say nothing of the changes in humidity of the air inside the chamber, with possibilities for deposition of water on the walls

<sup>1</sup> Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, p. 123.

<sup>2</sup> Hall, F. G., and R. W. Root, *Biol. Bull.*, 1930, **58**, p. 57.

of the respiration chamber) presents difficulties that make the measurement of the water-vapor output less accurate than that of the carbon-dioxide production. On the other hand, in long experiments such as we made with snakes, in which a condition of equilibrium was reasonably well established at the beginning and the end of the experiment and oil seals were used both for the respiration chamber and for the spirometer, the water vapor removed by the ventilating air current may be considered as that actually given off by the body of the subject. This is especially true in fasting experiments, when there is a minimum excretion of feces and urine. So many factors enter into the elimination of water vapor, that it is difficult to isolate any particular one. Probably measurements of the insensible perspiration of these cold-blooded animals would furnish important evidence regarding these factors. A few such measurements were carried out with the 1931 python and the 1930 tortoises and will be discussed later. (See pages 123 and 350.) Inasmuch as any discussion of the method of heat *loss* of these snakes must take into account the output of water vapor, and since, in the last analysis, carbon-dioxide production and oxygen consumption have their greatest value as indices of heat *production*, the observations with regard to the water vaporized will be presented first in our consideration of the respiratory exchange of snakes.

In all the experiments the water vapor was determined by direct absorption by sulphuric acid in a suitable absorbing vessel, usually a so-called "Williams bottle." With *large* respiration chambers it has always been our custom to determine at the beginning and the end of each period the water vapor inside the chamber, that is, the degree of humidity. This is done either by direct analysis of the air by passing a definite volume over sulphuric acid and pumice stone in U-tubes or, perhaps less accurately, by inserting a wet and dry bulb psychrometer in the ventilating air circuit. The air entering the respiration chamber invariably was absolutely dry. The air leaving the chamber will indicate its degree of saturation by depression of the temperature of the wet bulb thermometer. In the experiments with snakes it was not considered necessary to determine the degree of humidity at the beginning and the end of each experiment, since the water vapor was of secondary importance. It must be assumed, therefore, that the water vapor in the respiration chamber was the same at the beginning and the end of the periods of observation with snakes and that which we report as water vapor was the water actually absorbed in sulphuric acid during the period and weighed.

With warm-blooded animals the water vapor has recently been shown to bear a close relationship to the total metabolism, for the water vaporized from the lungs and skin (at least in conditions of rest) is in relatively constant proportion to the total insensible loss and this total loss is closely correlated with the heat production.<sup>1</sup> With cold-blooded amphibians the moisture of the skin may vary greatly according to how recently the animal has left the water. Hence the loss of water under these conditions is

<sup>1</sup> Benedict, F. G., and H. F. Root, Arch. Intern. Med., 1926, **38**, p. 1; Benedict, F. G., and C. G. Benedict, Biochem. Zeitschr., 1927, **186**, p. 278.

obviously disturbed. A typical case with a warm-blooded animal would be the hippopotamus. In earlier observations of the skin temperature of the hippopotamus<sup>1</sup> it was found necessary to have the animal out of the water tank for at least 6 hours in order for the skin to be at any reasonable degree of dryness. Most of the cold-blooded animals studied in this research, however, were animals living in the air, although prior to being placed inside the respiration chamber they had access to a water tank in which they could submerge themselves. It is believed that the moisture content of the skin of these animals was essentially uniform.

The rapid and profound changes in the body temperature of these large snakes, accompanying changes in environmental temperature, made it necessary to insure that in any studies of water vapor a constant temperature should have been attained before the measurements began. Hence in our discussion of the water vaporized by snakes only those experiments will be considered in which the animal had been sufficiently long at a constant environmental temperature to assure us that the body temperature and likewise the skin temperature were not undergoing any significant alteration. As was noted in the preceding section, under these conditions the rectal temperature of the snake is somewhat below the environmental temperature and the skin temperature is considerably below, 2 degrees or more. This of itself speaks for a large vaporization of water from the skin or surface of the snake, and hence the non-incubating snake may properly be compared to a wet bulb thermometer.

#### WATER-VAPOR OUTPUT WITH UNCHANGING ENVIRONMENTAL TEMPERATURE

An early inspection of our data obtained with snakes seemed to suggest that, because the rectal temperature is below that of the environment under constant conditions of environmental temperature, all the heat produced by the snake must be given off as heat of vaporization. This view was apparently substantiated by our unsuccessful attempt to measure directly the heat production of a snake. One of the snakes (boa N) was brought to the Nutrition Laboratory in Boston and placed inside an electrical compensation calorimeter.<sup>2</sup> It was found that this animal's heat production could not be measured directly. No heat as such was given off to the environment. The compensation chamber was actually too warm and could not be cooled. Simultaneous measurements of water vapor showed a large output of water vapor, indicating that the major portion, if not all, of the heat produced by the snake left the body by the path of vaporization of water. If the snake had been placed in a water bath in a large type of micro-calorimeter, such as that used by Hill or Rubner, direct heat measurements could have been obtained. But the vaporization

<sup>1</sup> Benedict, F. G., E. L. Fox, and M. L. Baker, Amer. Journ. Physiol., 1921, **56**, p. 464; *ibid.*, Proc. Nat. Acad. Sci., 1921, **7**, p. 154.

<sup>2</sup> Benedict, F. G., Boston Med. and Surg. Journ., 1925, **193**, p. 807; *ibid.*, Bull. Soc. Sci. d'Hygiène Alimen., 1927, **15**, p. 172.

of water by boa N removed so much heat that there was no loss of heat by radiation.

If it is true that all the heat produced by the snake is given off as heat of vaporization, then the water vaporized should bear a close relationship to the carbon dioxide produced. To determine whether this argument holds, we have presented in table 21 a comparison of the water-vapor output and the carbon-dioxide production, simultaneously measured, in experiments with snakes during periods of no agitation, no handling, no transition in environmental temperature during the experiment itself and for several hours beforehand, and with full ventilation of the respiration chamber (6.5 to 8.5 liters per minute). Although no record was made as to the exact time when the snakes were fed prior to these experiments, it is believed that they were all substantially in the post-absorptive condition. For purposes of comparison the values for the carbon-dioxide production and the water output have been computed per kilogram of body weight per 24 hours. These are average values for a number of consecutive periods on the given dates.

Examination of the data in table 21 shows that in general for every gram of carbon dioxide produced per kilogram of body weight per 24 hours, approximately 5 grams of water vapor per unit of weight and time were given off from the body of the snake. In other words, there is usually, although not invariably, a rough approximation to correlation between the carbon-dioxide production and the water-vapor output. As the carbon-dioxide production increases the water vapor also increases, and in most cases this increase is associated with an increased environmental or rectal temperature. At first it was our belief that the relationship between the production of carbon dioxide and the elimination of water vapor by the snake is so close that we could argue that the entire heat produced by the snake is lost by vaporization of water. If this close relationship actually exists, this is a further argument in favor of using the carbon-dioxide measurement as an index of the heat production. But subsequent analysis of our data in table 21 will show that the assumption that the snake's entire heat production is lost by vaporization of water is unproved.

The heat production has been calculated from the carbon-dioxide production, on the basis that each gram of carbon dioxide exhaled corresponded to the production of 3.325 calories, that is, that the respiratory quotient was 0.72. From this computed heat production has then been calculated the theoretical amount of water that would have been vaporized, if all the heat produced had been given off in the vaporization of water. For this calculation it has been considered that for each gram of water vaporized, 585 gram-calories (the latent heat of vaporization of water at 20° C.<sup>1</sup>) are needed. Comparison of the water vapor calculated from the heat production and the water vapor actually measured indicates that the agreement between the two is anything but satisfactory. Almost invariably there was actually much less water vaporized than would be accounted for by the assumption that all the heat produced was lost by

<sup>1</sup> Smith, A. W., *Phys. Rev.*, 1907, **25**, p. 145.



vaporization of water. With boa II, for example, in the first and the last experiments the actually measured water vapor is reasonably close to the calculated amount, but in the second experiment the measured loss of water should have been twice as much in order to equal that calculated from the carbon-dioxide production. Explanation of this great discrepancy

TABLE 21—*Comparison of carbon-dioxide production and water-vapor output of snakes in periods of no agitation, no handling, and no transition in environmental temperature*

Date	Snake and time	Body weight	Temperature of—		Per kilo. per 24 hours		
			Envi- ronment	Rectum	Carbon dioxide	Water vapor	
						Meas- ured	Calcu- lated <sup>1</sup>
1920	Boa N:	kg.	°C.	°C.	gm.	gm.	gm.
Feb. 18	9.34 a.m.—10.34 a.m.	10.15	35.80	.....	1.58	7.78	9.0
Feb. 18	10.34 a.m.—1.54 p.m.	10.15	36.00	.....	1.66	9.01	9.4
Feb. 18	1.54 p.m.—4.54 p.m.	10.15	36.20	.....	1.70	13.60	9.7
Feb. 19	9.21 a.m.—12.21 p.m.	10.08	34.8	.....	1.67	11.02	9.6
Feb. 19	12.21 p.m.—4.31 p.m.	10.08	34.9	.....	1.43	10.07	8.2
1921	Boa II <sup>2</sup> :						
May 11–14	12 noon —10.45 a.m.	5.98	22.62	22.52	.384	2.07	2.2
May 17	12.30 p.m.—12.01 a.m.	.....	17.39	.....	.455	1.33	2.5
May 18–20	4.30 p.m.—10.45 a.m.	5.56	17.74	.....	.229	1.41	1.3
	Boa III:						
May 26–29	3.30 a.m.—2.30 p.m.	6.01	20.98	21.82	.261	1.26	1.5
June 1–4	12.15 a.m.—2.00 p.m.	5.98	24.64	24.92	.394	1.39	2.2
June 6–8	1.30 a.m.—2.30 a.m.	5.95	27.23	.....	.537	1.95	3.1
June 8–9	6.00 p.m.—10.45 a.m.	.....	29.60	.....	.659	2.30	3.8
June 9–11	10.45 a.m.—11.00 a.m.	.....	29.96	29.77	.750	2.57	4.3
	Two small boas:						
June 14–15	2.00 a.m.—6.00 p.m.	4.48	23.79	.....	.485	3.66	2.8
June 28–29	2.05 a.m.—7.00 p.m.	4.42	24.79	.....	.526	3.66	3.0
	Boa IV:						
June 20–21	2.00 a.m.—11.30 a.m.	5.95	24.66	.....	.375	2.03	2.1
July 7–8	1.30 a.m.—11.30 a.m.	5.90	25.64	.....	.425	1.98	2.4
July 19–22 <sup>3</sup>	1.55 a.m.—10.30 a.m.	5.84	24.21	24.51	.570	2.29	3.2

<sup>1</sup> Calculated from carbon-dioxide production, assuming a respiratory quotient of 0.72 and 585 gram-calories for each gram of water vaporized.

<sup>2</sup> Boa II shed skin on May 14, after experiment was ended.

<sup>3</sup> Boa IV about to shed July 18; not known when it did shed.

is not simple. With boa III the water actually measured is in all cases considerably below that computed to have been given off, provided all the heat was given off as water vapor. Of itself this series of experiments with boa III could be taken as an argument against the notion that the heat produced is all lost by vaporization of water. In the experiments

with the two small boas, the measured water vapor agrees fairly well with the calculated amounts. Much the same can be said with regard to the results obtained with boa IV, although in general the water vapor actually measured is less than that computed.

The snake has not simply a source of heat within the body itself, but can actually absorb heat from the environment, and either of these sources of heat can facilitate the vaporization of moisture. To apportion the source of heat for vaporization of water between heat absorbed from the environment and heat produced within the body is out of the question in these experiments. Had the actually measured water vapor been much greater than that calculated from the carbon-dioxide production, one could easily account for the difference on the ground that extra heat was absorbed from the environment. Such heat absorption can of itself vaporize water, independent of any heat production. The body temperature of a dead snake, for example, would fall off to a certain extent but would not continually decrease and the snake's body would lose water in absorbing heat from the environment. When the measured water vapor is lower than the calculated, as with boa III particularly, the inference is that the body temperature was materially above the environment. This was not the case with boa III, however. Thus, in three of the experiments with this boa the rectal temperature was measured at the end of the experiment. In two instances the rectal temperature was only slightly above the environmental temperature and in the third instance it was actually somewhat below. The rectal temperatures recorded in table 21 are not, however, directly comparable with the environmental temperature, for the body temperature was measured at the end of the series of measurements in each case, whereas the values for environmental temperature represent averages for the whole period of measurement.

In view of this analysis of our data, it is believed that the relationship between the carbon-dioxide production and the water-vapor output is not so close as to represent a further argument in favor of using the carbon-dioxide measurement as an index of the heat production of snakes. Water vapor itself, therefore, becomes simply one of the factors in the heat loss of a snake, a factor complicated by the fact that the actual amount of heat required to vaporize the water will be in part the heat produced by the snake and in unknown part the heat absorbed by the colder snake from the slightly warmer environment. It is clear from this incomplete study that observations on the insensible perspiration of snakes are necessary, particularly with reference to the relationship between the carbon-dioxide production and the water vaporized, and with reference to the time of shedding the skin and the character of the integument. Such observations would be important in throwing light upon the methods of heat regulation and heat loss of these cold-blooded animals. Thus far no technique has been developed for measuring separately the loss of water from the skin of the cold-blooded animal and that from the lungs. The water vapor leaving the lungs with the carbon dioxide exhaled can be computed approximately. For this computation one must know the amount of

carbon dioxide exhaled and the humidity of the inspired air and must assume that the air leaving the lungs would be saturated with water vapor at the temperature of the animal itself. Again one would have to assume that the ventilation rate was approximately uniform per liter of carbon dioxide exhaled. Further, it must be assumed that the respiratory center of these animals reacts with the same degree of stimulation as does that of man. All of these assumptions, however, are so doubtful as to make such speculations at this time unprofitable. But it is obvious that, because of the rôle played by the vaporization of water in the loss of heat, the skin area of the cold-blooded animal is a really important factor in the regulation of the body temperature. The heat regulation of cold-blooded animals is therefore deserving of further intensive study.

#### WATER-VAPOR OUTPUT AS AFFECTED BY DIFFERENT ENVIRONMENTAL TEMPERATURES

In the experiments reported in table 21, in which the water vapor given off by snakes was determined, the snakes had in all cases been under a constant environmental temperature for several hours beforehand, so that they were in a uniform state. On February 18 and 19, 1920, experiments were made with a boa (boa N) at a high temperature, 35° or 36° C. Deferring for the present the discussion of the carbon-dioxide output at different temperatures, we can see that the water vaporized per kilogram of body weight per 24 hours was on the average of the two days not far from 10 grams. This is a much higher value than those found in subsequent experiments in 1921 with other boas at distinctly lower environmental temperatures. A high environmental temperature thus has a noticeable effect on the water vaporized by the snake. Perfect correlation between the water vaporized per kilogram of body weight per 24 hours and the environmental temperature is, however, not found, for with boa III on June 8 to 9 and June 9 to 11, when the environmental temperature was about 30° C., the water vapor was only about 2.5 grams or one-fourth that at 36° C. There is evidence in much of our work that between 30° and 36° C. there may be a critical temperature for water elimination. On more than one occasion we have taken snakes out of a warm environmental temperature and found them distinctly moist. The presence of sweat glands as such in the snake has not been demonstrated. Indeed, their absence has been the basis for argument<sup>1</sup> that the vaporization of water must be accomplished largely by the lungs. From the relationship between the carbon-dioxide excretion and the water-vapor output, especially under varying conditions of environmental temperature, it is hardly probable that the large amounts of water involved in the snake's metabolism can be lost solely through the lungs and it appears that the skin, in spite of the absence of sweat glands, still furnishes a large supply of water vapor.

<sup>1</sup> Wetmore, A., Smithsonian Misc. Coll., 1921, 72, pp. 12 and 22.

### WATER VAPOR AS AFFECTED BY AGITATION

That the water vapor may be affected by conditions other than environmental temperature is shown by the experiments with boa N. On February 20, 1920, at an environmental temperature of 23° C., the water vaporized per kilogram of body weight per 24 hours was 11.33 grams, or not far from that on the two preceding days (see table 21) when the environmental temperature was nearer 36° C. That the water vaporized at 23° C. was not lower than that at 36° C. is explained by the fact that prior to the experiment on February 20 the snake had been in a wire tube preparatory to some body-temperature observations, had been handled excessively for measurements of length and girths, and the agitation incidental to this handling had by no means disappeared at the beginning of the respiration experiment. This experiment proves that agitation has an effect on the excretion of water vapor.

### INFLUENCE OF VENTILATION RATE (RELATIVE HUMIDITY) ON WATER VAPORIZED BY SNAKES

Under the conditions of experimenting, air entered the respiration chamber absolutely dry, having been passed over sulphuric acid. Consequently, although no direct measurements of the relative humidity of the air in the chamber were made, it could be assumed that the more rapid the ventilation the drier was the air. Several experiments were made in the series of water-vapor determinations in which the environmental temperature was unchanged during the period of measurement but the ventilation rate was altered greatly. Knowledge regarding the water vapor per kilogram of body weight per 24 hours with varying ventilation rates is of importance in determining whether changes in humidity have any influence upon the elimination of water vapor. Our data show that in three periods with a boa weighing 6 kg., at an average environmental temperature of 26.3° C., and with a ventilation rate of 8 liters per minute, the water vaporized per kilogram of body weight per 24 hours was 2.11 grams. In seven periods with the same snake at the same environmental temperature, but with a ventilation rate of but 2 liters per minute, the water vapor was 2.10 grams, that is, there was no change. With two small boas (combined weight 4.48 kg.) in the chamber it was found that in two periods at the higher rate of ventilation (8 liters) and at an environmental temperature of 23.1° C., the water vapor per kilogram of body weight per 24 hours was 3.48 grams. In four periods at the lower ventilation (2.5 liters), at the same temperature, the water vapor was 3.32 grams, a slight decrease. Seven periods with these two snakes at 24.31° C. and with a ventilation of 7 liters per minute gave 3.73 grams of water vapor, and six periods at the same temperature but with a ventilation rate of 2.5 liters gave 3.72 grams. From these comparisons it can be seen that the lower degree of humidity necessarily accompanying the more rapid ventilation (a ventilation four times as great as the slower rate) was without any effect on the water vaporized by the snakes. It is unfortunate that the actual relative humidity was not recorded. We have reason to believe that at the higher rate of ventilation the humidity must have been very low.

### INFLUENCE OF SHEDDING THE SKIN UPON LOSS OF WATER VAPOR

The profound change taking place during the shedding of the skin of serpents suggests the possibility of an alteration in the water exchange of the skin during this period. Certain of our data were obtained toward the terminal stages of shedding. A boa weighing 4.14 kg. was studied at an environmental temperature of approximately 21° C., in a number of periods covering three days, and the water vapor given off per kilogram of body weight per 24 hours averaged 5 grams. This boa was about to shed and the scales came off and stuck to the hands, as the rectal temperature was taken. At the end of the fourth day, but not during a period of measurement, feces were passed in the chamber, so the boa was taken out, the chamber cleaned, and the animal put back. On the next two days, at the same environmental temperature, an average of 11 grams of water vapor per kilogram of body weight per 24 hours was obtained in five periods. Thus with the snake, there is evidence of a highly increased water output during the shedding stage, in spite of the absence of sweat glands. On the last day, during a period following these five periods, feces were passed and during this period the water vapor rose to 23 grams per kilogram of body weight per 24 hours, this increment being without doubt in very large part due to the water vaporized from the excreta.

Another boa was studied that was about to shed. The eyes were coated and blue, and the belly was blue. Five periods covering the time from 11<sup>h</sup>30<sup>m</sup> a.m., June 1, to 8<sup>h</sup>30<sup>m</sup> p.m., June 2, gave on the average 4 grams of water vapor per kilogram of body weight per 24 hours. This is much lower than the values noted with the serpent mentioned above, although the body weight in this second case was 3.40 kg. as compared with 4.14 kg. in the first case. The environmental temperature was about 21° C. It is clear by reference to table 21 (page 118) that the excretion of even 4 grams of water vapor per kilogram of body weight per 24 hours is much higher than that noted at about 21° in the experiments recorded in table 21.

These two instances give fairly distinct evidence to the effect that the shedding process, or at least the onset of the shedding process, results in a considerably increased vaporization of water. Fortunately the rectal temperatures were taken in all the periods of observation. With the first serpent, especially during the periods when the high loss of water was noted, the rectal temperature was frequently 2 or even 3 degrees lower than the environment. In the second instance, where the water vapor was much less than in the first, but still higher than normal, the rectal temperature was only slightly below the environment. With the vaporization of as much as 10 to 12 grams of water vapor per kilogram of body weight per 24 hours there is a profound lowering of the rectal temperature, and the snake has distinctly the characteristic of a wet bulb thermometer. It would appear that just prior to the shedding period there is an unusually large loss of water vapor, resulting in a pronounced depression of the body temperature of the snake. Just what rôle this plays in the physiology of

the shedding of the skin is not clear at present. The results of these experiments do point out, however, the significance of water vapor as a means of heat loss in these animals.

### INSENSIBLE PERSPIRATION AND WATER OF VAPORIZATION OF THE 1931 PYTHON

From experience with many warm-blooded animals it is obvious that insensible perspiration is affected to a certain extent by the environmental temperature and particularly by the intensity of the metabolism, such as the high metabolism directly reflecting the after-effect of digestion. Consequently in the study of the insensible perspiration of the 1931 python (this type of measurement was not made on any of our other cold-blooded animals except the tortoise—see pages 350 to 353) a number of factors had to be taken into consideration, such as environmental temperature (both dry bulb and wet bulb), the length of time after the ingestion of food, the possible effect of agitation and handling prior to the observations, and the possible effect of wind movement. In the course of the two months of experimentation with the 1931 python a large number of body weight measurements were secured, notably measurements of the insensible loss in body weight, but these were so interwoven with the factors mentioned above that a clear picture of the effect of each different factor is only with difficulty obtained. The first series of determinations of the insensible perspiration began on January 10, the python remaining suspended from the balance continuously from 9<sup>h</sup>05<sup>m</sup> a.m. on this day until 8<sup>h</sup>43<sup>m</sup> a.m. on January 12. The results of this and the following series of measurements are recorded in table 22. A Sauter balance of 10-kg. capacity was used, capable of weighing accurately to the nearest centigram.

The accuracy of the determination of the insensible perspiration is proportional to a certain extent to the length of the period. Frequently the periods were short, and any error in weighing would therefore be appreciable. It is furthermore probable that, in spite of seeming lethargy, the snake was perceptibly disturbed by the presence of the operator at the time of the weighings. Indeed, at times, although not invariably, audible deep respiration or hissing was heard. In short periods the effect of this agitation would be greater than in long periods. During long periods extending throughout the night such agitation would play the smallest rôle. Fortunately during the series from January 10 to 12 there were two overnight periods, one 773 minutes and the other 853 minutes long. During these overnight periods the insensible perspiration amounted to approximately 4 grams per kilogram of body weight per 24 hours. This may be taken as approaching the basal or standard insensible perspiration of the python at an environmental temperature (dry bulb) of 25° or 26° (wet bulb, 14° to 15°). This value of 4 grams does not, however, necessarily represent the insensible perspiration under conditions of complete fasting, since the snake had been fasting only from 112 to 135 hours, which, although a long time for a warm-blooded animal to fast, represents but a relatively short time in the digestive cycle of the snake. Hence this in-

sensible loss of 4 grams was undoubtedly somewhat complicated by the after-effect of digestion.

During the 2-hour period and the immediately following 7-hour period on the afternoon of January 11 an electric fan was blowing air over the

TABLE 22—*Insensible perspiration of 1931 python*

Date and body weight	Hours after food	Time	Length of period	Environmental temperature		Insensible loss per kg per 24 hrs.
				Dry bulb	Wet bulb	
1931			<i>mins.</i>	<i>°C.</i>	<i>°C.</i>	<i>gm.</i>
Jan. 10...	88	9.05 a.m.	...	26.3	18.0	....
5529 gm.	89.5	10.50 a.m.	105	25.7	18.0	6.57
	90	11.14 a.m.	24	26.3	18.3	3.58
	92	1.12 p.m.	118	26.0	17.3	5.56
	93	1.57 p.m.	45	26.7	14.9	5.67
	94	2.50 p.m.	53	26.5	14.9	4.28
	95.5	4.33 p.m.	103	26.3	15.9	4.32
	99.5	8.37 p.m.	244	26.7	14.9	5.63
Jan. 11...	112.5	9.30 a.m.	773	26.5	14.9	4.21
5502 gm.	114.5	11.30 a.m.	120	27.3	15.4	15.06
	121.5	6.30 p.m.	420	27.5	....	15.42
Jan. 12...	135.5	8.43 a.m.	853	25.3	14.2	3.99
5478 gm.						
Jan. 28...	87.5	9.43 a.m.	...	32.0	18.6	....
6407 gm.	88	10.16 a.m.	33	32.4	19.2	28.30
	88.5	10.42 a.m.	26	33.4	19.3	7.28
	89	11.13 a.m.	31	33.4	19.0	7.03
	90	11.46 a.m.	33	33.3	18.8	7.51
	90.5	12.16 p.m.	30	33.1	18.7	7.30
	91	1.10 p.m.	54	34.4	18.5	18.43
	92	2.06 p.m.	56	33.9	17.8	7.33
	92.5	2.41 p.m.	35	33.7	17.8	7.43
	93	3.08 p.m.	27	33.9	18.0	7.26
Jan. 30-31	143.5	5.17 p.m.	...	32.6	17.1	....
6577 gm.	158.5	8.40 p.m.	923	32.4	17.3	16.74
Feb. 7....	328.5	10.29 a.m.	....	20.6	8.8	....
6237 gm.	331.5	1.22 p.m.	173	20.4	8.2	<sup>3</sup> .67
	334	4.14 p.m.	172	19.3	8.2	.42
	337.5	7.21 p.m.	187	19.5	10.2	.43
Feb. 8....	351.5	9.40 a.m.	859	20.0	11.2	.35
	356	2.10 p.m.	270	19.6	11.6	.26
Feb. 9....	375	8.48 a.m.	1118	20.5	10.7	.55

<sup>1</sup> Electric fan blowing air over snake during this measurement.

<sup>2</sup> Rectal temperature measured at 9<sup>h</sup>15<sup>m</sup> a.m., Jan. 28.

<sup>3</sup> Rectal temperature measured at 9<sup>h</sup>45<sup>m</sup> a.m., Feb. 7.

snake, and the insensible loss per kilogram of body weight per 24 hours during these two periods was 5.06 and 5.42 grams, respectively. Comparison of these values with the approximately basal value of 4 grams obtained in the two overnight periods indicates that the violent movement of air over the snake resulted in a definite increase in the vaporization of water. This strengthens our belief that the snake has to a certain extent the nature of a wet bulb thermometer.

Handling would be expected to result in a somewhat higher insensible loss than quiet repose, and it is to be noted that in the first period on January 10 the insensible perspiration was 6.57 grams per unit of weight, that is, the highest of any of the values in the series, and undoubtedly it reflects the after-effect of handling prior to the experiment.

A second series of observations on the python was made from 9<sup>h</sup>43<sup>m</sup> a.m. to 3<sup>h</sup>08<sup>m</sup> p.m. on January 28. The periods were short, varying from 26 to 56 minutes in length. The dry bulb temperature averaged 33.3° and the wet bulb temperature 18°, or notably higher than in the preceding experiment. In the first period the rate of insensible loss was high, 8.3 grams, because of previous handling. Thereafter during all but the sixth period it averaged 7.3 grams per kilogram of body weight per 24 hours. During the sixth period between 12<sup>h</sup>23<sup>m</sup> and 1<sup>h</sup>06<sup>m</sup> p.m., that is, for nearly three-quarters of an hour, air was blown over the snake by an electric fan and the insensible loss increased to 8.43 grams, but in the following periods when no air was blown over the snake the loss again reached a level of approximately 7.3 grams. In this experiment, as in the first, there is a clear indication of an increase in the vaporization of water as a result of wind movement.

On January 30 a respiration experiment with the python ended at 4<sup>h</sup>13<sup>m</sup> p.m. In order that the snake should not be disturbed before the next day's experiment it was left in its box, the box resting on the laboratory floor. To insure ventilation, a blast of air from an electric fan was directed through a funnel into the box throughout the night. The insensible loss was determined during the night of January 30 to 31 in a 15-hour period, at an average dry bulb temperature of 32.5° and a wet bulb temperature of 17.2°. It was found to be 6.74 grams per kilogram of body weight per 24 hours, a value agreeing well (taking into consideration the 2-degree difference in temperature) with that obtained in the short period on January 28, when the fan was also blowing air over the snake.

The insensible loss was determined in an experiment at a lower temperature, about 20°, on February 7 to 9. The experimental periods were approximately three hours long, though some were longer, one being 19 hours long. The insensible loss computed per kilogram of body weight per 24 hours varied considerably in this experiment, from a minimum of 0.26 to a maximum of 0.67 gram. Before the experiment the python had been at a low temperature, for the recording thermometer showed that at one time during the night of February 6 to 7 the temperature had been 13°. The animal had been placed in its box and left on the laboratory floor on the evening of February 6 and had not been handled since that time until 9<sup>h</sup>45<sup>m</sup> a.m., February 7, when its rectal temperature was taken. It is possible that the first high insensible loss of 0.67 gram may reflect the effect of this handling. If the high value of 0.67 gram is ruled out, the other values range from 0.26 to 0.55, showing that the insensible perspiration at an environmental temperature of about 20° was much less than that at 26° or 33°. The snake, however, had been without food long enough to have reached the true fasting stage.



In general, the insensible loss of this python per kilogram of body weight per 24 hours was about 0.4 gram at 20°, 4.0 grams at 26°, and 7.3 grams at 33°. Since the python weighed not far from 6 kg., the total 24-hour loss would be about 2.4 grams at 20° and 24 grams at 26°, or ten times greater. At 33° it would be nearly 50 grams. It is impossible to approximate natural conditions with these animals in the laboratory. It is clear that air movement plays a rôle in the insensible loss. On the other hand, the degree of humidity to which the snake was subjected during its stay in the laboratory in the winter months was evidently much lower than would be found in its natural habitat, particularly when the temperature is high. Sufficient evidence is at hand, however, to show that the water of vaporization plays an important rôle in the total heat economy of these cold-blooded animals.

It may be assumed, for purposes of discussion, that the insensible loss in weight of the snake represents entirely loss of water. This assumption is certainly debatable, and there seems to be some evidence that there may be a retention of oxygen as a result of possible intermediate oxidative processes. But on the basis of this assumption it is interesting to compare the total 24-hour insensible loss of this python of approximately 50 grams at 33° C. with the water loss of the ordinary human. The total insensible perspiration of the normal adult human would average not far from 720 grams per 24 hours.<sup>1</sup> This is nearly 15 times the amount lost by the serpent. The serpent, however, weighed 6 kg. and the average adult human would weigh 60 kg. or ten times as much. Thus it is obvious that at the temperature of 33° (which approaches, although it is not actually the same as, the human body temperature) the water loss of the cold-blooded snake per kilogram of body weight may approximate that of the warm-blooded human. Another interesting comparison between the cold-blooded and the warm-blooded animal is the effect of wind movement on the insensible perspiration. With humans the water loss is not appreciably altered when air is blown over the body, whether the body is clothed or nude,<sup>1</sup> but with the python our data show that wind movement results in a material increase in the water of vaporization or the insensible perspiration.

During many of the periods when the respiratory products of the 1931 python were measured inside the respiration chamber the water vaporized by the snake was collected and weighed. The determination of the water vaporized has two special uses in the study of these cold-blooded animals; to give information concerning (1) the water actually vaporized, considered as a product of the metabolism or as a loss from the body itself contributing toward the water metabolism or the water balance, and (2) the rôle of water vapor as a path for the loss of heat, for we believe that a large part of the heat lost from the body of the cold-blooded animal or, under certain conditions, all the heat lost from the body is lost through the vaporization of water. Finally, measurements of the water vaporized are of interest because the water vaporized would be expected to have a fairly definite relationship to the insensible perspiration. It so happened,

<sup>1</sup> Benedict, F. G., and C. G. Benedict, *Biochem. Zeitschr.*, 1927, **186**, p. 278.

unfortunately, that we could not simultaneously determine with the necessary accuracy the insensible perspiration, the water of vaporization, and the gaseous metabolism. On the days when the insensible perspiration was measured, we had to forego the direct determination of the water vapor and the gaseous metabolism. On the other hand, the environmental temperature was always well known, and hence the relationship between the water given off as such, the insensible perspiration, and the metabolism in general can be treated.

For purposes of discussion it may be considered that if the total heat production is known, the probable water output can be computed on the assumption that the entire heat produced is lost by means of the water of vaporization. In table 23 have been recorded the measurements of the water actually vaporized per kilogram of body weight per 24 hours during the various respiration experiments made with the 1931 python. For purposes of comparison there are also given the calculated amounts of water that would have had to be vaporized to bring away all the heat produced during the metabolism experiments. These last values have been computed from the indirectly measured heat production (table 55, p. 208) on the basis that each gram of water vaporized is accompanied by the loss of 585 gram-calories. The environmental temperature recorded in table 23 is the temperature that prevailed inside the respiration chamber during the measurement of the water vapor and the gaseous metabolism. The rectal temperature was taken after the respiration experiment ended. The environmental temperature noted at the time the rectal temperature was determined is shown in tables 11 and 56 (pages 81 and 211).

The python was fed on January 24, following the measurement of the water vaporized, and the dates from January 27 through February 3 are considered to represent the period of digestion. Inspection of the data in table 23 shows that the amounts of water vaporized seem to be in large part independent of the digestive activity. If the days affected by digestive activity are not taken into consideration it can be seen that, although the amounts of water actually vaporized vary considerably with the temperature of the environment, in general the lowest amounts were found at the low temperatures and the highest at the high temperatures. This was not always the case, because at the high environmental temperature of 35.4° on February 4, the water vaporized amounted to only 3.14 grams, whereas on February 20 when the temperature was 35° or practically the same, the water vaporized was 5.26 grams. It is true, however, that the maximum amount of water vaporized was 6.18 grams on February 24, when the highest environmental temperature prevailed. On the five days when the environmental temperature was as low as 17° or 18°, less water was vaporized, although the variability was again great, *i.e.*, from 1.35 grams on January 19 to 0.57 gram on February 26. In general, the water of vaporization follows fairly directly the environmental temperature, and the larger amounts are vaporized at the high temperatures.

Perhaps the most striking feature of table 23 is the comparison of the water actually vaporized with the water calculated as having been vaporized to take care of the entire heat produced, as measured by the gaseous

metabolism. This comparison shows extraordinarily discordant results. On only a relatively few days is there even an approximate agreement between the two sets of values. On January 19 and 20 at the low en-

TABLE 23—Comparison of water vaporized by 1931 python as actually measured and as calculated from indirectly measured heat production

Date	Temperature of—		Water vaporized per kg. per 24 hours	
	Environ- ment	Rectum	Measured	Calculated from heat produced <sup>1</sup>
1931	°C.	°C.	gm.	gm.
Jan. 14	25.8	....	2.72	4.57
Jan. 15	22.2	22.7	2.36	3.06
Jan. 16	24.5	....	2.31	3.04
Jan. 17	24.4	24.7	1.86	2.70
Jan. 19	18.2	....	1.35	1.55
Jan. 20	20.0	14.3	1.71	1.83
Jan. 21	31.6	31.0	3.67	5.25
Jan. 22	31.4	31.4	4.97	5.19
Jan. 23	24.9	24.7	2.44	2.75
Jan. 24	25.3	25.1	4.39	3.09
Jan. 27	31.9	35.6	<sup>2</sup> 6.04	36.21
Jan. 29	31.3	....	4.51	22.99
Jan. 30	31.1	....	4.29	13.11
Jan. 31	32.9	34.0	<sup>3</sup> 4.90	15.46
Feb. 2	30.9	32.5	<sup>3</sup> 3.04	9.81
Feb. 3	31.4	....	3.00	6.33
Feb. 4	35.4	38.7	3.14	11.70
Feb. 6	31.3	33.1	1.54	4.79
Feb. 9	18.0	....	.63	1.14
Feb. 10	18.8	18.9	.74	1.24
Feb. 12	17.6	....	1.09	1.33
Feb. 13	31.9	30.6	1.69	5.07
Feb. 18	29.1	29.4	2.64	4.20
Feb. 19	32.4	33.1	3.78	5.44
Feb. 20	35.0	36.2	5.26	7.85
Feb. 21	36.1	36.1	4.48	6.91
Feb. 24	38.1	37.9	6.18	7.77
Feb. 26	17.4	17.3	.57	1.36

<sup>1</sup> Assumed that all the heat produced was lost as water vapor and that 1 gm. of water was vaporized for each 585 gram-calories lost.

<sup>2</sup> Not measured simultaneously with carbon-dioxide and oxygen measurements, but immediately following such measurements.

<sup>3</sup> Includes one observation on water vaporized after respiration experiment proper had ended.

vironmental temperature there is close agreement. On January 22 there is good agreement. But after January 24 the water vaporized, as actually measured, is considerably lower than that calculated from the heat produced. The snake was fed at 5 p.m. on January 24, following the water-vapor determination. On January 27 and 29 and on February 4 and 6 the discrepancy between the measured and the calculated amounts

of water is pronounced, but thereafter there is a tendency for the two values to approach each other more nearly as time goes on. The natural inference is that sensible heat is given off by the snake, and that the water vaporized does not account for all the heat produced. Against this, however, are the results of experiments with this python by direct calorimetry on February 16 and 17, which will be discussed subsequently (see p. 423). These direct calorimeter experiments showed that at two distinctly different environmental temperatures the python in repose produced no sensible heat. It is clear from this study that the relationship between the water vapor and the heat loss of the snake, particularly during and after digestion, is by no means definitely established. With the snake the vaporization of water as a physical path for the loss of heat represents a much larger proportion of the total heat developed than is the case with humans. Man and many animals, at least under basal conditions, lose only from 20 to 25 per cent of their heat as a result of vaporization of water. It is regretted that this problem could not have been studied further. The two calorimeter experiments with this python, as far as they go, are extremely illuminating, although the calorimeter itself was not designed primarily to measure such small quantities of heat as are represented in the metabolism of these cold-blooded animals.

A comparison may be made of the water vaporized per kilogram of body weight per 24 hours as actually measured and recorded in table 23 and the insensible perspiration per unit of weight as recorded in table 22. For this purpose the results for the actually measured water vapor (not including those obtained during the period of digestion, *i.e.*, from January 27 through February 3) have been plotted with reference to the environmental or rectal temperature of the snake in figure 33. All the values for water vapor obtained at temperatures below 25° have been plotted with reference to the temperature prevailing inside the respiration chamber at the time the water vapor was determined and are indicated as dots. Those obtained at temperatures above 25° (indicated as crosses) have been plotted with reference to the rectal temperature of the snake, since at the higher temperatures the rectal temperature is somewhat below the environmental temperature. The dots and crosses representing data obtained before the ingestion of food on January 24 have been enclosed in circles. The three average values for the insensible perspiration, of 0.4, 4.0, and 7.3 grams at 20°, 26°, and 33°, have been plotted as dots enclosed in squares. It will be noted instantly that at 20° the insensible perspiration is measurably lower than any line that could be laid through the plotted points for water vapor to represent the general trend. At 26° the insensible perspiration is slightly higher than the general trend for the water vapor, and at 33° much higher. To what extent the more sensitive, more keenly alert snake at the higher temperatures was cognizant of the movements of the operator in obtaining the weights at the higher temperatures, and to what extent this influences the insensible perspiration it is difficult to tell. The disturbing presence of the operator was probably not without influence. The insensible perspiration is, however, on the whole measurably above the water vaporized, and one recalls instantly that the

calculated amount of water necessary to absorb all the heat produced was likewise above the measured water vapor. Hence it may be concluded that, in general, the insensible perspiration tends to approximate the values for the calculated water output. Since simultaneous determinations of insensible perspiration and actual weighing of the water output were not

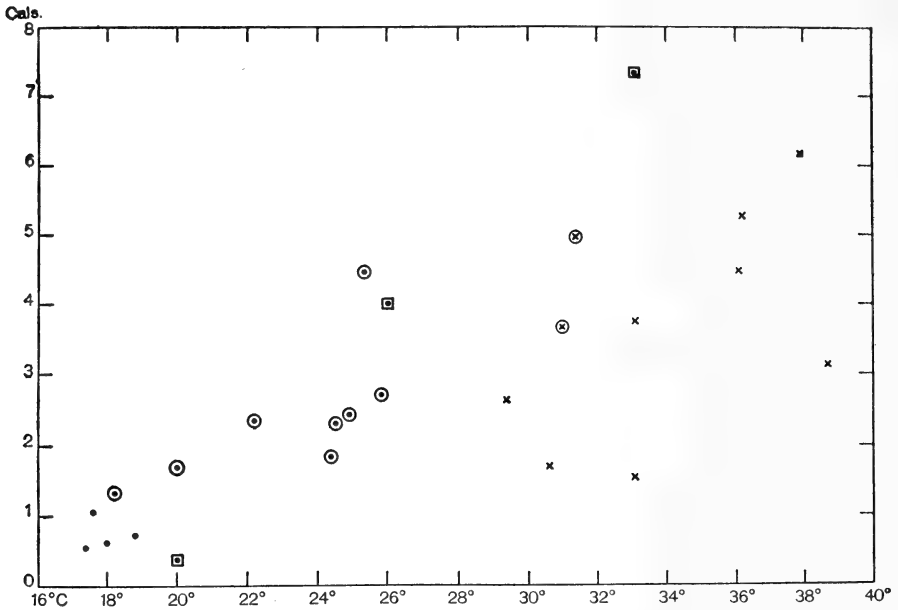


FIG. 33—COMPARISON OF WATER OF VAPORIZATION AND INSENSIBLE PERSPIRATION OF THE 1931 PYTHON PER KILOGRAM OF BODY WEIGHT PER 24 HOURS.

Dots enclosed in squares represent insensible perspiration. Dots enclosed in circles represent values for water vapor obtained before ingestion of food and plotted with reference to environmental temperature. Dots not enclosed in circles represent values obtained after ingestion of food and plotted with reference to environmental temperature. Crosses enclosed in circles represent values obtained before ingestion of food and plotted with reference to rectal temperature. Crosses not enclosed in circles represent values obtained after ingestion of food and plotted with reference to rectal temperature.

feasible and strikingly different conditions obtained in the two sets of measurements, this apparent accord is probably not of real biological significance.

### THE SOLID AND LIQUID EXCRETA OF THE SNAKE

The urine and the feces of the snake are frequently passed together or nearly simultaneously. In many instances they are passed when the snake is agitated or handled, and it has been thought by some observers that in such cases the excreta were voided as a means of defense, since their odor at times is very bad. It was not intended to include in this research

a study of the intermediary metabolism<sup>1</sup> of the snake or a study of the excreta, but during the course of the digestion experiments with snakes at the New York Zoological Park our interest in the composition of snake's excreta was aroused by the obviously fatty nature of the feces that were voided when the snakes were forcibly fed with beef fat. Hence in a few instances these feces were collected, weighed and analyzed to verify the ocular impression of the excessive fat content. Subsequently, when the 1931 python was being studied, a few samples of excreta were likewise collected. These were analyzed at the Nutrition Laboratory for their water, ash and fat content, and Professor Otto Folin of the Harvard University Medical School determined their nitrogen content and made other observations regarding them. We wish here to express to him our deep appreciation of his cooperation in these analyses.

In the New York experiments it was difficult to collect all the feces passed during any one digestive cycle, and no method was worked out to separate the feces ascribable to a certain food ingestion. Six different samples were analyzed, all obtained during the fat-digestion experiments. The results are given in table 24. On June 10, 1918, a sample of feces (sample 1) from boa G was collected. Boa G on May 16 had been fed 227 grams of beef fat wrapped in a 57-gram rabbit pelt, and had been studied in the respiration chamber from May 16 to May 30. During the collection of the feces approximately 30 grams were lost. The actual amount collected was 314 grams. There was no record of other feces passed during this digestive cycle. Since the amount lost can be only crudely estimated, and since it is uncertain whether other feces were passed during the digestive cycle, no attempt has been made to correct the results of our analyses for this uncollected mass, and the percentage values reported for sample 1 in table 24 are based only upon the collected amount of 314 grams. This amount, when dried in a hot-air bath, finally reached an air-dry weight of 147.7 grams. On June 12 boa G was fed 340 grams of beef fat plus 43 grams of rabbit pelt. The only specimen of feces collected following the ingestion of this food was passed on June 26 (sample 2) and weighed 161 grams. This was subsequently dried to 111.6 grams and analyzed. On July 1 feces weighing 182 grams (sample 3) were passed by this same boa, presumably belonging to the digestive cycle following the fat ingestion on June 12. Unfortunately no record was made, however, as to whether this animal was fed again between June 12 and July 1. Since in the May digestion experiment this boa had been fed on May 16 and feces were not passed until June 10, and since in the June digestion experiment it was fed on June 12 and feces were passed on June 26, it is highly probable that the feces collected July 1, that is, only five days after those of June 26, are ascribable likewise to the fat feeding of June 12. On December 20, 1919, boa J passed 348 grams of feces (sample 4). It had been fed 198 grams of beef fat and 28 grams of rabbit pelt on December 5. In this particular case there were some lumps of fat in the feces that had obviously

<sup>1</sup> The interesting suggestions of Szretter, regarding the protein utilization of fasting snakes, are worthy of serious consideration. See Szretter, R., *The Hunger Metabolism of Fasting Snakes*, Travaux de l'Institut Nencki, Varsovie, 1922, 1, No. 31.

undergone no noticeable change. Boa J was fed again on December 30, being given 227 grams of beef fat and 57 grams of rabbit pelt. Feces weighing 127 grams were passed on January 12. These were not analyzed. The boa ate three dead rats on January 12 and passed feces again on January 18-19. This collection of feces (sample 5) was sent to Boston for analysis, but was not analyzed until considerably later. One other sample of feces (sample 6) was collected, but unfortunately no record was made regarding which animal passed them or what the fresh weight was. They were characterized as containing a large proportion of hair, and were known to be a normal fecal excretion. The analyses of these samples of feces reported in table 24 indicate a large percentage of fat due to the forced feeding of fat. The last sample, which consisted chiefly of hair,

TABLE 24—*Composition of feces of snakes*

Sample No.	Fresh weight	Air-dry weight	Per cent of air-dry sample			
			Water	Fat	Ash	Nitrogen
	<i>gm.</i>	<i>gm.</i>				
1	314	147.7	2.20	77.3	4.37	2.42
2	161	111.6	....	86.9	....	2.67
3	182	139.8	....	87.1	....	5.51
4	348	....	....	<sup>1</sup>	....	....
5	133	....	7.67	24.5	36.4	4.01
<sup>2</sup> 6	...	....	5.88	0.13	29.3	3.08

<sup>1</sup>Contained 180 grams of fat, or 51.7 per cent on fresh basis.

<sup>2</sup>Contained 49.8 per cent of hair on air-dry basis.

was probably a true residual product representing the indigestible hair. This sample had a low fat content and a high ash content. By the method of washing, we were able to determine that approximately half of the dry weight was hair.

In these studies of feces we were dominated first by the fatty nature of these excreta and hence we laid emphasis upon the first five samples, believing that they represented a real fecal discharge. Sample No. 6 was so obviously made up, in large part, of hair as to represent probably the normal feces of the snake uncontaminated, so to speak, by large masses of fat. Subsequent experience with the 1931 python leads us to believe that the normal feces will have a relatively high ash and low fat content, whereas the solid urine will have a markedly different composition. These six samples therefore unquestionably represent feces.

The 1931 python was kept in an Abderhalden metabolism cage, the bottom of which was formed of iron rods. Any liquid urine passed fell immediately into a box below the cage, and the solid excreta were of such form, usually like a ball or bolus, that they remained in the cage. In figure 34 is shown a photograph (taken February 3) of the 1931 python with three boluses of excreta lying beside it, voided just before the photograph was taken. Rather badly out of focus in the immediate foreground,

at the left, is a mass of whitish, chalklike substance that was passed first by the animal. Professor Folin found that this mass contained 82 per cent of uric acid. The other two masses near the snake were brown in color and different in texture. To show the segment-like form of these masses of feces, a closer view of a sample of true feces, laid on paper ruled in square inches, is given in figure 35. These masses obviously contained a large amount of hair. Each bolus was about the size of two walnuts with a fairly sharp plane marked off at each end, as if they had been in a tube

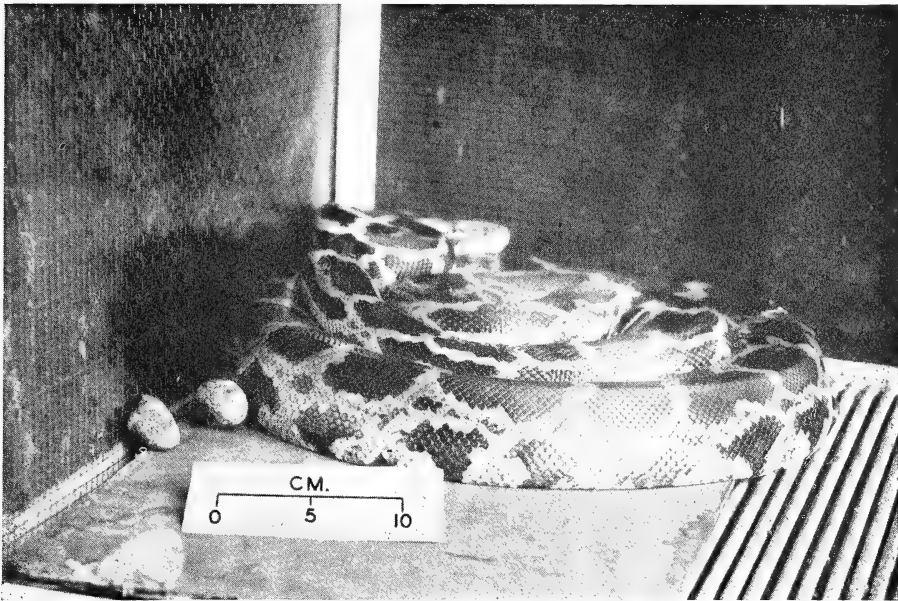


FIG. 34—1931 PYTHON IN AN ABDERHALDEN METABOLISM CAGE WITH EXCRETA RECENTLY PASSED.

The two masses of excreta near snake were brown in color. In immediate foreground at left, out of focus, is a whitish, chalklike mass which was found on analysis to contain 82 per cent of uric acid.

and had been cut off or separated, much as the segments, for example, in the normal feces of the horse or in those of the steer after long fasting.

The 1931 python was fed two guinea-pigs on January 24. Subsequently, on being handled, it passed considerable excreta. On January 31 liquid urine was voided, collected, and later analyzed by Professor Folin. The solid excreta passed on February 5 were definitely white and chalklike, as are commonly found in zoological parks. On February 13 solid excreta were passed, amounting to 49 grams. The samples analyzed for February 5 and February 13 proved, from their chemical composition, to be solid urine. On February 14 a large mass of feces, not unlike those of the dog, were passed. These contained some hair. Two weeks later (February 27) when the animal was taken to the roof of the Laboratory for photographs, three balls of feces amounting to 47 grams were passed. At the time of dis-



section of this snake (March 4) 25 grams of feces in two boluses were removed from the intestinal tract. No other intestinal contents were noted.

The several samples of excreta collected from the 1931 python were analyzed, some only in part and some rather fully (table 25). Thus, the only analysis made of the samples obtained on February 27 and March 4 was with regard to the ash content. In the fresh substance of February 27 the ash content was 2.05 per cent and on March 4 it was 3.27 per cent. Chemically the solid excrements differed from each other. That on Feb-

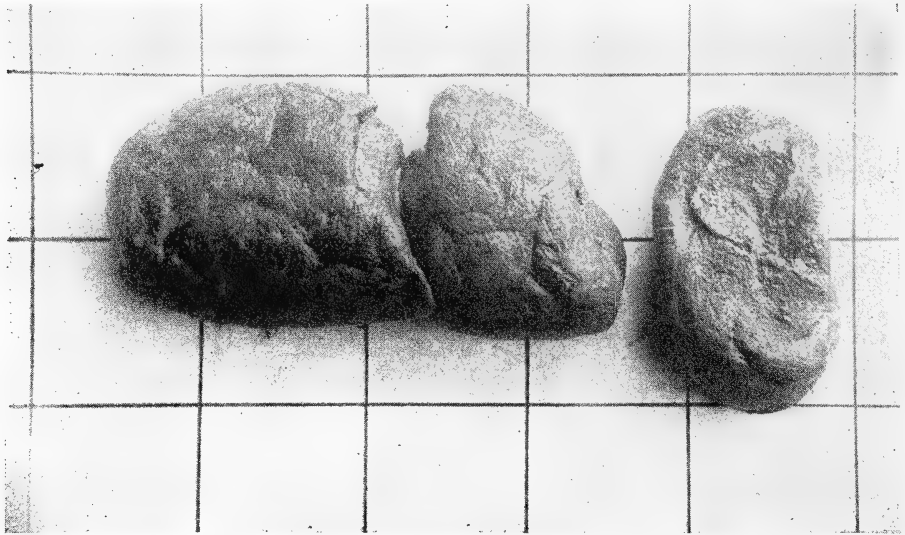


FIG. 35—NORMAL, HAIR-CONTAINING FECES PASSED BY THE 1931 PYTHON.

Squares are one inch (25 mm.) on each side.

ruary 5 was chiefly uric acid, with a small amount of ash and fat. These small percentages of ash and fat point to a urinary rather than a fecal excretion. The normal feces were represented by the sample on February 14, which consisted of a large amount of hair and had a large percentage of ash. This is in conformity with the analysis of the last sample listed in table 24, which contained 29 per cent of ash. This ash content is probably more nearly representative of the normal feces of the snake, as distinguished from the urine and as distinguished from the so-called "fatty feces" which represent a wholly special condition.

The two samples of February 27 and March 4 were obviously of a fecal rather than a urinary nature. In the March 4 specimen fourteen of the python's teeth were found. On the other hand, the percentage of ash in both of these samples is very low, much lower than that in the sample for February 14, true feces, and likewise lower than that in samples 5 and 6 in table 24. Although the presence of teeth seems to make it clear that we were dealing with feces rather than urine, it is obvious that a more elaborate analysis of these two samples should have been made.

Of the liquid urine voided, that on January 31 was dark brown in color, indeed almost black. It was uncontaminated by feces but had been in contact with the galvanized iron walls of the respiration chamber. It was found to react strongly acid to litmus paper. Liquid urine passed on February 13 reacted neutral to slightly alkaline, and urine passed on February 10 gave a very slight alkaline reaction. Professor Folin analyzed a sample of the urine voided on January 31 and likewise made analyses of the excreta passed on February 5, 13 and 14. He reported that the specimen of January 31 (volume 175 c.c.) "had a specific gravity of only 1.014. It was black in color, but this dark color seemed to be due to material in suspension rather than in solution. The reaction with alkaline picrate was so weak that at the most there could not have been over 35 mg. of creatinine present, and the character of the reaction was so atypical

TABLE 25—*Composition of solid excreta of 1931 python*

Date	Kind of excreta	Fresh weight	Air-dry weight	Per cent water lost in drying	Per cent of air-dry sample		
					Fat	Ash	Nitrogen
1931		<i>gm.</i>	<i>gm.</i>				
Feb. 5	Urine	42.6	31.1	27.0	0.35	1.11	35.6
Feb. 13	Urine	49.2	....	....	....	....	29.0
Feb. 14	Feces	161.4	58.2	64.0	6.25	43.9	3.7
Feb. 27	Feces	47.4	....	....	....	<sup>1</sup>	....
Mar. 4	Feces	25.4	....	....	....	<sup>2</sup>	....

<sup>1</sup> Per cent of ash in fresh feces, 2.05.

<sup>2</sup> Per cent of ash in fresh feces, 3.27.

that I do not think any of the reducing material was really creatinine. The total nitrogen was 603 mg. and of this, 170 mg. were present as ammonia nitrogen. There was no urea present. There were 172 mg. of ammonium salt. The ammonium salt was probably mostly that of some organic acid, for the organic acids were equivalent to 133 c.c. of tenth normal acid. Tests for lactic acid were negative. The large amount of ammonia was not due to decomposed urea, because the urine was still slightly acid in reaction. The total amount of uric acid was 159 mg. There were present phosphates (inorganic) equivalent to 163 mg. of P. One of the curious features of the urine is the fact that of the 271 mg. of total sulfate-sulfur present, all but 26 mg. (less than 10 per cent) were present as ethereal sulfate."

Of the bulky solid excrements, Professor Folin examined only the cleanest, which was practically free from hair. It contained 82 per cent of uric acid. He repeated several of the determinations on two other samples of urine. These gave results which agreed substantially with what was obtained from the first, and hence only the figures for the urine of January 31 are reported.

As seen on the gravel beds of the various snake departments in zoological parks, the excreta of the snake usually appear like fairly large, whitish

balls or masses of dry, chalklike consistency. Although our observations of snake's excreta were of a wholly incidental nature, at least four types of excreta were noted: (1) A white, chalklike mass, found to be largely uric acid; (2) a mass heavily impregnated with fat, the result of digestion experiments with fat, which we have designated as "fatty feces"; (3) a brownish mass consisting in large part of hair, evidently true undigested food material; and (4) a liquid excreta which may be called urine. Judged from their chemical composition, the white, chalklike masses are in all probability not a fecal but a urinary excretion or at least a product of protein metabolism. The brownish, hair-containing masses represent the true, normal feces and contain a large percentage of ash. The liquid urine was found to have a chemical composition wholly unexpected, owing to the presence of a large amount of ethereal sulfate. A liquid excreta from snakes has in general not been recognized by most writers, probably because on the beds of the dens (which are usually warm) there is considerable gravel and the urine will rather rapidly vaporize. Indeed, until 1931 our own observations on snake's excreta were confined to the solid and semi-solid excreta found in the cages. In handling the snakes, not infrequently large voidings of liquid were noted. If the snake is placed in an Abderhalden cage, however, any liquid passed will immediately fall to the bottom of the cage and there it can be collected in a suitable vessel. It is hardly reasonable to think that in an animal that drinks as the snake is known to drink (for the water needed for its metabolism is by no means confined to that obtained when bathing) there would be such a fine proportionality between the water of vaporization and the water drunk that there would be no liquid excreta. The 1931 python frequently passed liquid excreta when in the Abderhalden cage.

Most of our samples of snake's excreta were collected with the obvious intent of studying the so-called "fatty feces" and therefore contained a large amount of fat. We analyzed so few samples of normal feces, that it would be unprofitable and only speculative to compare the normal feces with the fatty feces. The securing of information regarding the mechanism for the discharge of these various types of excreta, their serial order in the digestive cycle, and their chemistry<sup>1</sup> calls for far more study than the Nutrition Laboratory had time to engage in, owing to the large amount of other experimental work on hand. Our observations are admittedly fragmentary and serve chiefly to show the great number of lacunæ existing in the knowledge of the excretory products of the snake. Originally it was hoped to secure some information with regard to the digestibility of fat with the snake, to clarify the problem of the "specific dynamic action" of fat, but it was uncertain whether all the fatty feces for the particular digestive cycle studied had been collected, and some feces were lost in a number of instances when the snakes smeared the feces in such a manner as to make a complete collection impossible. The observations here cited are therefore given more as a matter of record than as a complete solution of any of the great problems in the intermediary metabolism

<sup>1</sup> The chemistry of the feces of snakes formerly played an important rôle in certain pharmaceutical operations.

of serpents. If these fragmentary observations serve no other purpose than to call the attention of biochemists and physiologists to the importance of a further study of the excreta of the snake, this result will fully compensate for the labor involved in the analyses here reported.

The earlier literature concerning the excreta of reptiles has been cited by Ellinger.<sup>1</sup> There is also an article by Roberts<sup>2</sup> on the urine of serpents and an article by Lewis<sup>3</sup> on some analyses of the urine of turtles and alligators. As far back as 1862 Hastings<sup>4</sup> published an account of an inquiry into the medicinal value of the excreta of reptiles, in which he commented on the chemical composition of the excreta.

## BODY MEASUREMENTS OF SNAKES

### BODY SURFACE AND SKIN AREA

The custom of comparing the heat production of living animals on the basis of the surface area, although universal in the case of warm-blooded animals, has not generally been applied to cold-blooded animals in anything like a convincing manner. Seemingly the snake is the simplest of all living forms for the direct measurement of surface area. To be sure, the head is slightly more irregular in configuration than the tail, and yet there are no extremities such as legs or wings, no ears of unusual shape, and no recesses. The body is not an elongated cylinder nor yet is it really two elongated cones with their bases together, but nevertheless it has such a fairly simple geometric design that, theoretically, it would seem as if the surface area of a snake could be fairly accurately determined by measuring the length and a number of girths. At first sight it would seem that the best method would be to remove the snake's skin and measure its area by a planimeter or some similar instrument. This was done only in the case of the 1931 python. It was undesirable to kill the other snakes for this purpose, and with two exceptions they had to be measured while alive. Of the snakes used in metabolism experiments before the 1931 python, body measurements were made on two pythons, four boas and two rattlesnakes. The measurements consisted of the total length from the tip of the nose to the tip of the tail and a number of girths, obtained with a steel tape measure. The girths were measured along the length of the body at intervals usually of from 10 or 15 to 30 or 60 cm., depending upon the size of the snake. It was fully realized that by this method of measuring the girths any change in traction on the tape would affect the girth readings and therefore the computation of the body surface. Hence every effort was made to secure uniform traction, in so far as possible. The results of these measurements, including the body weight of the snake at the time of measurement, are recorded in table 26. These data give some hint as to the state of nutrition of these snakes.

<sup>1</sup> Ellinger, A., Oppenheimer's Handb. d. Biochem., 1910, **3** (1), p. 540.

<sup>2</sup> Roberts, W., *On the Chemistry and Therapeutics of Uric Acid Gravel and Gout*, Croonian Lectures, London, 1892.

<sup>3</sup> Lewis, H. B., *Science*, 1918, n.s., **48**, p. 376.

<sup>4</sup> Hastings, J., *An Inquiry into the Medicinal Value of the Excreta of Reptiles in Phthisis and some other Diseases*, London, 1862, p. 7.

TABLE 26—*Body measurements of snakes*

Snake, date, weight, and total length	Girth measurements		Snake, date, weight, and total length	Girth measurements	
	Distance from nose	Girth		Distance from nose	Girth
	<i>cm.</i>	<i>cm.</i>		<i>cm.</i>	<i>cm.</i>
Large python:	30	21	Boa C:	15	15
Mar. 16, 1916	69	28	Mar. 22, 1916	46	20
31.8 kg.	122	38	12.45 kg.	91	32
491.5 cm.	183	41	289.6 cm.	137	36
	274	36		183	25
	335	30		229	18
	396	26		274	9
	427	22	Boa D:	10	18
	488	8	Apr. 4, 1917	15	15
Large python:	38	22	13.21 kg.	46	21
Mar. 20, 1916	76	27	293.4 cm.	76	27
31.8 kg.	122	37		107	28
495.3 cm.	168	39		137	31
	213	42		168	32
	259	39		198	28
	305	34		229	23
	366	28		259	13
	427	21		284	7
	493	7	Boa G:	7	15
Small Indian python:	8	13	Apr. 4, 1917	15	11
Apr. 6, 1917	15	10	9.3 kg.	46	19
7.34 kg.	46	17	242.6 cm.	76	25
253.4 cm.	76	22		107	30
	107	27		137	31
	137	27		168	26
	168	22		198	20
	198	23		229	7
	229	14	Boa H:	8	17
	244	6	Apr. 4, 1917	30	16
Rattlesnake:	<sup>1</sup> (5)	<sup>1</sup> (15)	7.46 kg.	46	18
Mar. 19, 1916	<sup>1</sup> (9)	<sup>1</sup> (10)	243.8 cm.	61	26
4.59 kg.	30	15		76	28
<sup>2</sup> 185.4 cm.	61	22		91	26
	91	24		107	27
	122	22		122	27
	152	17		137	25
	180	8		152	23
				168	23
Rattlesnake:	5	15		183	21
July 3, 1917	9	12		198	19
3.49 kg.	30	13		213	17
<sup>3</sup> 180.3 cm.	46	17		229	10
	61	21		236	6
	76	22			
	91	22			
	107	22			
	122	19			
	137	17			
	152	13			
	168	9			
	173	6			

<sup>1</sup> Assumed.<sup>2</sup> Includes 5 cm. for rattle.<sup>3</sup> Includes 7 cm. for rattle.

No attempt was made to measure the girths and the length of the 1931 python while it was alive, since it was realized that it was ultimately to be sacrificed. However, on the day of autopsy, after the snake was chloroformed, measurements were carefully made corresponding to those made with the earlier series of snakes. Since the traction of the tape plays such a rôle in these measurements, two different observers determined the girths at given distances from the nose of the snake and recorded their

TABLE 27—*Comparison of girths and breadth of skin of 1931 python, based on measurements of body after death and of skin laid on cross-section paper.*<sup>1</sup>

Distance from nose	Measurements of—		
	Body girths		Skin breadth
	Observer A	Observer B	
<i>cm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>
15	105	108	147
30	131	131	149
45	159	158	181
60	207	208	218
76	214	209	222
91	214	213	229
107	216	215	223
122	214	213	222
137	207	205	218
152	195	198	218
168	185	189	213
183	179	183	209
198	166	169	198
213	142	145	190
229	75	77	183
244	35	34	171
259	...	...	147
274	...	...	70
290	...	...	35
Average	165	166	181

<sup>1</sup> Length before skinning, 247 cm.; length of skin, 297 cm.

observations independently. The results are shown in table 27. There was no question with regard to the length of the snake, although a certain degree of stretching could have been introduced if one had tried to stretch the animal. The snake's body was straightened without any tension whatsoever, laid out as straight as possible on a board covered with cross-section paper ruled in square inches (fig. 36), and the length was found to be 247 cm. Figure 37 is a photograph of the 1931 python, taken while it was still alive, to show its length in comparison with a man having a stature of 183 cm. This photograph likewise shows (as does figure 38) that, although the 1931 python was subjected several times to

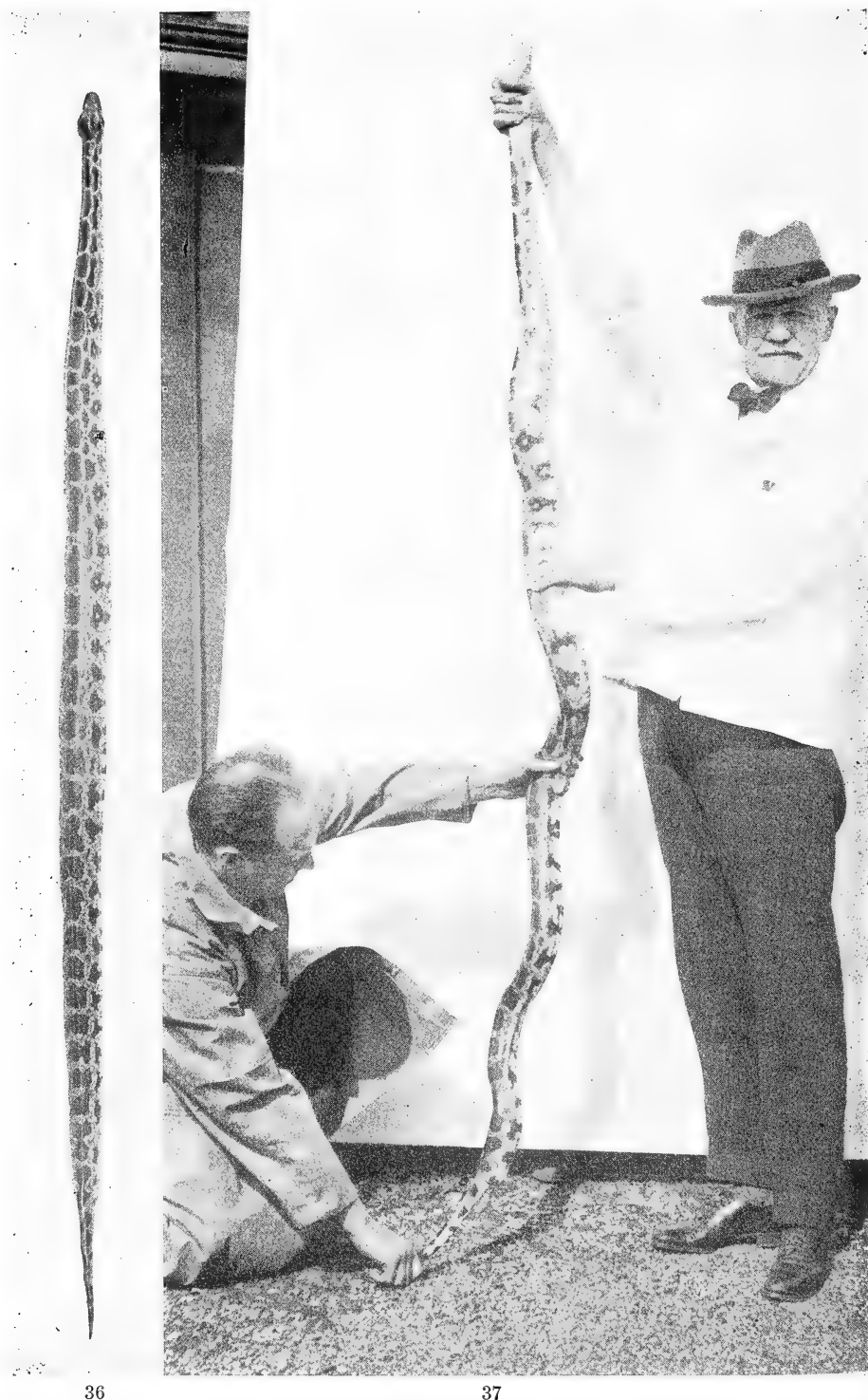


FIG. 36—1931 PYTHON STRETCHED OUT ON SQUARE INCH PAPER AFTER ITS DEATH, TO MEASURE ITS LENGTH.

FIG. 37—THE 1931 PYTHON (ALIVE) HELD AS NEARLY AS POSSIBLE WITHOUT TWISTS IN ITS BODY, TO COMPARE ITS LENGTH WITH HEIGHT OF A MAN OF 183 CENTIMETERS.

temperatures as high as  $37^{\circ}$  or over, it still had plenty of vitality, as evidenced by its obvious muscular contortions.

*Skin area*—The skin of the 1931 python was removed immediately after it had been chloroformed and its area directly measured. To remove the skin of a large snake and measure its area accurately was no simple task, and yet it was accomplished in the following way. A smooth board, wider than the snake's skin would be when laid out flat and longer than the snake, was covered with a number of sheets of cross-section paper ruled in one-inch squares and carefully matched end to end. Upon this the



FIG. 38—ACTIVITY OF THE 1931 PYTHON AFTER EXPOSURE TO  $37^{\circ}$  C.

Photograph, taken at end of experimental series with python, after it had been subjected several times to temperatures of from  $36^{\circ}$  to  $38^{\circ}$  C., shows snake still capable of active movement.

snake's skin was laid. The snake's body was slit down its entire ventral length and the skin gently lifted or separated from the rest of the body tissue with a sharp knife, with extraordinary precaution to avoid any tension or traction on the skin that would tend to stretch it. After removal, the skin was at no time lifted at one end or in the middle but was rolled up from the tail to the head, then laid upon the board, unrolled from the head to the tail, gently patted into position without any stretching, in so far as possible, and held in place on the board with thumb tacks. The skin was photographed in this position in two sections (fig. 39), so as to enable subsequently more accurate measurements of the skin area from the photograph by means of a planimeter. The removal of the skin around the neck and jaws resulted in two flaps, which are prominent in figure



39. Near the tail two small sections of skin were lost, when the vestigial pelvic appendages were cut out for another purpose. In computing the area, however, allowance was made for these two missing portions of skin. An outline was drawn around the skin with a pencil on the cross-section paper to indicate the skin area, and then the skin was removed and added to the other parts of the body for subsequent analysis of the body composition. The cross-section paper was next carefully dried with a hot flat iron to prevent any wrinkling or stretching due to moisture. The actual area enclosed in the traced outline of the snake's skin was determined by counting the number of square inches and fractions of a square inch on the cross-section paper and converting the total to square centimeters or square meters. The skin area as thus determined was 0.53 square meter. The photograph of the skin was likewise measured with a planimeter and the skin area was found to be the same by this method.

It was observed that in spite of every possible precaution to prevent stretching of the python's skin, the length of the skin was 297 cm. after it was removed from the body, as compared with the original length, 247 cm., of the dead snake before being skinned. Thus the skin had actually stretched 50 cm. in length while being removed from the animal's body.<sup>1</sup> It was conceivable that this lengthening might have been at the sacrifice of the width and hence that the area as such had not been materially altered. With this in mind, the width of the skin was measured after it had been laid flat on the cross-section paper, the attempt being made to obtain these measurements at the same distances from the nose as those at which the girths were measured before the snake was skinned. These widths are also shown in table 27, and it can be seen that, in spite of the care taken to prevent stretching of the skin, it had not only stretched in length but likewise in width or girth. These data give evidence of the extreme difficulty of removing the skin from a snake and not unwittingly stretching it, or they may indicate that there is a tendency for the skin to relax completely after death and thus result in a greater area.<sup>2</sup>

After a number of preliminary calculations of the surface area from these measurements of lengths and girths given in tables 26 and 27, it was concluded that the best method was to assume that the snake is made up of a series of sections shaped either like a trapezoid or a truncated cone. The tail end was thought of as shaped like a cone and the area was computed by multiplying the perimeter of the base (the girth nearest the tail) by half the slant height of the cone, represented by the distance

<sup>1</sup> The distensibility of the skin of the snake can hardly be over-emphasized. F. Doflein (*Tierbau u. Tierleben, II: Das Tier als Glied des Naturganzen*, Leipzig and Berlin, 1914, p. 150) gives an illustration of a python that has just swallowed a pig, which indicates the extent to which the skin can be stretched. Barbour, in his most interesting book on *Reptiles and Amphibians* (New York, 1926, fig. 40) reproduces this difficultly accessible illustration. It is well known that the skin of the living serpent after digestion retracts to its normal size. It is not at all inconceivable that with tonus missing in the dead animal, the skin can easily be inadvertently stretched and will not return to anything like its original normal size.

<sup>2</sup> The rôle played by the stretching of the skin has been interestingly discussed by Thomas (*Arch. f. Physiol.*, 1911, p. 36) and by Pfaundler (*Zeitschr. f. Kinderheilk.*, 1916, 14, p. 48).

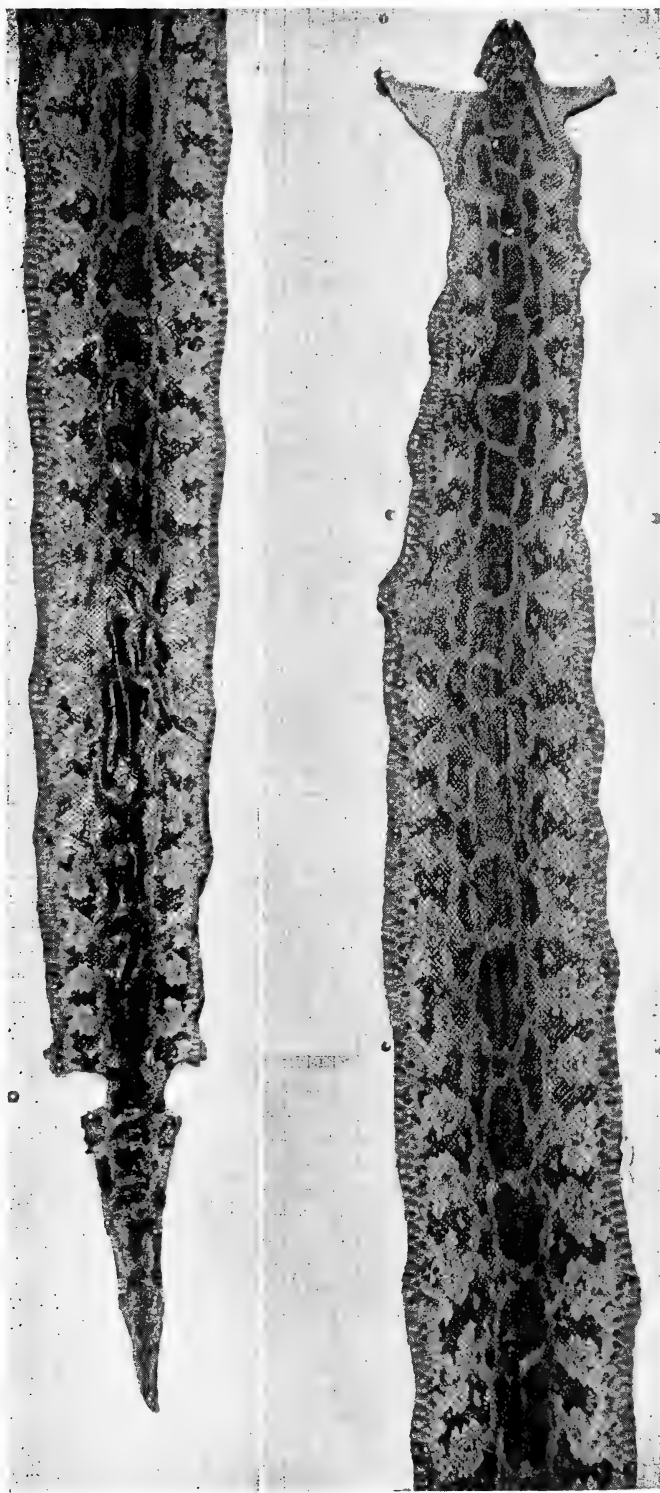


FIG. 39.—SKIN OF THE 1931 PYTHON LAID FLAT ON PAPER RULED IN SQUARE INCHES.

Two flaps near head represent loose skin under neck and jaws. Near tail two sections of skin are missing. These were removed when vestigial pelvic appendages were cut out. Upper and lower photographs have been cut at ends so that two sections of skin shown in these photographs match exactly end to end.

from the tip of the tail to that point along the snake's length where the girth nearest the tail was measured. The head was not assumed to be shaped like a cone, because the noses of these snakes were somewhat blunt. The head section therefore and all the other sections between the head and the tail sections were considered to be made up of two trapezoids each, the snake being visualized as split open down its length and spread out flat. The area of each section of two trapezoids was computed by multiplying the length of that particular section (the distance between the two given girths of the snake) by the sum of the two given girths (the girths representing the parallel sides of the two trapezoids). The girth at the end of the nose of the snake was not measured, but an assumption was made as to this girth. The computed areas for all these different sections were then added together to obtain the total surface area of the snake's body. (See table 28, page 146.) Another method of calculating the surface area from the length and the girths was tested in the case of boa H. The snake's body was considered to be made up for the most part of a number of cylinders, with the head as the frustum of a right cone and the tail as a right cone. The resulting surface area agreed within less than 1 per cent with the area calculated on the basis of the trapezoids.

With the smaller snakes the measurements were accomplished without great difficulty, for the operator could easily handle them. They could be stretched out and measured as desired. Two of them were measured after they were dead, namely, the small Indian python and the rattlesnake measured on July 3, 1917. The greatest difficulty was experienced with the largest python, weighing 31.8 kg. and having a length of 5 meters. As figure 40 shows, the services of five men were required to handle this animal, besides the person making the measurements. It was difficult to keep it straightened out. There were continually muscular movements, contraction and expansion of the muscles, and consequently the girths could be obtained only with a certain degree of error. Attention is called to this fact and also to the fact that a second series of measurements was made on this python, in order to obtain a check upon the computation of the surface area. In spite of the difficulty of securing the girth measurements, the two series gave almost the same surface area. It is believed, however, that among all the snakes measured the greatest errors in measurement, particularly in the girths (which in this type of calculation play an important rôle), occurred with the large python.

Although we were able to measure indirectly the surface area of nine snakes and to measure directly the skin area of one snake, it was desirable to obtain, if possible, a factor that, when applied to the two-thirds power of the weight, would give a close approximation to the measured surface area. Consequently the measured surface area was divided by the two-thirds power of the weight, and the factor  $K$  (in the formula  $S=K \times w^{2/3}$ ) obtained. The results of such calculations are shown in table 28, in which the weight, the length, the measured surface area, and the factor  $K$  are recorded. Comparison of the weights and the surface areas shows, as is to be expected, that the larger the animal the larger is the surface area. It so happened that no two animals had identically the same weight, so

that the measured areas can not be compared directly. The factor  $K$  recorded in the last column of the table ranges from 12.0 to a maximum



FIG. 40.—MEASURING LENGTH OF A 5-METER PYTHON WEIGHING 32 KILOGRAMS.  
Photographed by Mr. E. R. Sanborn, New York Zoological Park.

of 14.4, one of the two factors obtained with the large python. Except for the large python, however, the factor is fairly uniform for all the snakes. With the 1931 python the factor was 12.9 and 13.0, respectively, based upon the two series of girths obtained by two different observers. The agreement in these two results is extraordinarily close and only slightly

higher than the average of 12.5. The snakes measured varied greatly in weight from 3.5 to 32 kg., and yet the body-surface constant is essentially the same with all of them, although based on measurements taken independently at several different times by different observers. Hence the possibility of any personal equation playing a rôle is ruled out, and it would appear as if the technique of determining the surface area by measuring a series of circumferences and lengths was reasonably standardized.

The one existing body-surface constant for snakes thus far appearing in the literature is that found by Inaba.<sup>1</sup> Inaba has reported body-surface constants for five snakes ranging in weight from 48 to 109 grams. His individual values for *K* are 19.1, 17.0, 17.5, 18.7 and 19.9, and the

TABLE 28—*Body surface constants (K) for snakes, derived from actually measured body weight and surface area*

Snake	Length	Body weight	Body surface (measured)	Body-surface constant
	<i>cm.</i>	<i>kg.</i>	<i>sq. cm.</i>	
Small Indian python.	253.4	7.34	4877	12.9
Rattlesnake.....	185.4	4.59	3302	12.0
Rattlesnake.....	180.3	3.49	2903	12.6
Boa C.....	289.6	12.45	6474	12.1
Boa D.....	293.4	13.21	6725	12.0
Boa G.....	242.6	9.30	5476	12.4
Boa H.....	243.8	7.46	5147	13.2
1931 python.....	247.3	5.58	4097	13.0
Average.....	.....	.....	.....	12.5
Large python.....	491.5	31.80	14336	14.3
Large python.....	495.3	31.80	14435	14.4

average value is 18.6. Inaba's article gives every evidence of most careful work.<sup>2</sup> The agreement among the individual values for *K* is excellent, and there is no hint that there was any systematic technical error. We found it difficult, therefore, at first to understand the difference between his average value of 18.6 and our average of 12.5. There is one notable difference in the two series of snakes studied, that is, Inaba's snakes were all small, the maximum length being 84 cm., whereas our snakes were all large, the maximum length being 495 cm. That two animals of the same general configuration should not have areas approximately in the same proportion to the two-thirds power of the body weight is, however, inconceivable, especially when the general configuration is relatively so simple as that of the snake. Hence we were at first at a loss to understand why Inaba's constant should be so high when compared with ours.

<sup>1</sup>Inaba, R., Arch. f. Physiol., 1911, p. 7.

<sup>2</sup>Only after our body surface measurements with the 1931 python were made did we receive a private communication from Professor Karl Thomas that Inaba had especially laid out his snake skin so that the length of the skin was no longer than before the snake was skinned. This was apparently possible with Inaba's small snake, but we believe it could not have been done with our large python.

Inaba's values for  $K$ , however, were based on measurements of the snakes' skins after they had been removed. There is in Inaba's report no hint of any stretching of the skin, as is only too commonly and erroneously done in measurements of surface area of animals, and yet it seems as if such stretching, at least laterally, must have taken place. We are confirmed in this belief by the fact that the body-surface constant of our 1931 python was found to be 17.0, when based upon the measured skin area after the skin had been removed from the body, whether the photograph of the skin area was planimetered or whether the skin area was measured by counting the number of square inches and fractions of a square inch enclosed in the traced outline of the skin on the cross-section paper. This factor of 17.0 is somewhat smaller, to be sure, than Inaba's average value of 18.6 but measurably greater than the constant of 13.0 calculated from the length and girths of the python's body. The fact that the value for  $K$  for the 1931 python was distinctly greater both on the basis of planimentering the photographed skin area and counting the square inches enclosed in the traced outline on cross-section paper rules out the possibility of any error in planimentering, any error resulting from the possible distortion of the photograph by having the camera out of focus, or any error due to shrinkage of the cross-section paper in drying. It would thus appear as if the increase in the size of the constant were due to the stretching of the skin.

In order to compute the body surfaces of all the snakes that we experimented upon, we shall use a value of 12.5 for  $K$ , representing the average derived from the factors for all the measured snakes, excluding the large python. It is our belief that the factor for the large python is probably a little too large. Consequently it is not included in the average. The measured surface area of this large python is probably somewhat too large, inasmuch as the factor is larger than the average, but the measured surface area of this large python is retained in all the calculations of its heat production per square meter of body surface.

The surface area of the large python (see table 28) is striking, when compared with the surface area of a human. Thus, the area of the large python, which weighed but 32 kg., is 1.44 square meters or the same as that of a human 151 cm. tall and weighing 50 kg. In other words, the surface area of this python per unit of weight is large. This should be borne in mind especially, in the subsequent discussion of the heat production of this large python per unit of measured surface area.

In a few instances measurements were made of the metabolism of snakes, both when they were in a normal condition and when greatly emaciated. In one case (boa D) the animal had lost nearly half its initial body weight. It is unfortunate that the length and particularly the girths were not measured again on boa D in the highly emaciated state. The application of the factor 12.5 to the two-thirds power of the body weight of this emaciated animal must be made with considerable reserve, for it is not yet demonstrated that this factor would apply to a greatly emaciated animal. Experiments on this point should be made. But in view of the general appearance of the skin of an emaciated

snake, it is difficult to conceive how there could be a shrinkage in the skin area of the snake to correspond to the great loss of tissue due to extreme emaciation. The true surface area of the emaciated snake may therefore be not far from that obtaining during full nutrition and not the greatly reduced area that would result from the application of the factor 12.5 to the two-thirds power of the body weight of the emaciated snake. Measurements of the skin area of two snakes originally having the same length, weight and girths, one animal in a well-nourished state and the other nearly starved for comparison, would be a direct contribution to this problem of the effect of state of nutrition on skin area.

Perhaps no animal is so frequently folded upon itself with consequent reduction of actual surface area exposed to the temperature of the environment as is the snake, which is habitually coiled. Typical illustrations of such coiling are shown in figures 16 and 34 (pages 44 and 133). Because of this habit of the snake, probably the use of the surface area in any calculation of the snake's heat production is more inconsistent than with any other type of animal known. Indeed, one must continually bear in mind Rubner's injunction that skin area and surface for heat loss are two entirely different things.<sup>1</sup> In the attempt to prevent this coiling, we forced one of our snakes to enter a large wire-mesh tube (see page 63), in which there could be no folding of the body on itself. But this defeated our aims, in that the snake was then in contact with a highly conducting metallic surface. Rubner, by suspending the animal in a net, attempted to avoid this tendency for animals, such as the sleeping dog, to reduce their heat-losing surface by curling up. This procedure, however, has been by no means universal in metabolism measurements in studies of comparative physiology. Our use of these measured surface areas of snakes is in full cognizance of the fact that we know nothing of the amount of body surface actually exposed for heat radiation or, what is more important with snakes, the vaporization of water. However, since it seems to be important to compare the heat measurements of these cold-blooded animals (regarding which so little information is available) on every possible basis, we shall in a subsequent chapter report the heat production per unit of *computed* skin area, fully cognizant of the fact that the computed area does not represent the surface actually exposed to the environment.

#### COMPOSITION OF THE SNAKE'S BODY

In considering the nature of the metabolism of these cold-blooded animals and particularly in comparing them with warm-blooded animals, we believed it would be helpful to know something about the body composition of the snake, such as the percentage of water and fat in the body, the nature of the fat, and the weight of the skeleton. Consequently, following the autopsy of the 1931 python, which was kindly made for us by Dr. H. W. Rand of the Zoological Laboratory of Harvard University, some observations on body composition were secured. It was impracticable

<sup>1</sup> Rubner, M., *Beiträge zur Ernährung im Knabenalter*, Berlin, 1902, p. 40.

to carry out a complete chemical analysis of the body. Such an analysis, to be complete, should include separate analyses of the flesh, skin, fat and skeleton. But the water, ash and nitrogen content of the entire body were determined. After the autopsy, the entire body, including the skin and the skeleton, was put through a meat chopper several times. The ground material was then placed in enamel pans and dried in a hot-air bath (but never exceeding 80° C.) until it reached a reasonably constant weight. The material was then left in the air to assume an air-dry condition. Subsequently the ash and the nitrogen content were determined. These measurements represent far from a complete analysis and only accentuate the importance in future studies of more careful consideration of the chemical composition of the body of the animals that are used for experiments.

As the result of several well-agreeing analyses, the body of the 1931 python was found to contain on the average, on the fresh basis, 75.2 per cent of water. On the air-dry basis it contained 5.1 per cent of water, 23.8 per cent of ash, 8.26 per cent of fat and 9.88 per cent of nitrogen. It can be seen that the ash content was high and that there was a fairly liberal supply of fat in the body, although the snake had not been excessively fed and had been subjected to a fairly long fast. The value for the fat content, 8.26 per cent, in part confirms the results of the autopsy carried out by Dr. Rand, who reported:

"I can make no statement about the quantity of blood beyond the general statement that the blood was rather scanty. I was especially struck by the smallness of the heart, which was relatively much smaller than in turtles and in tortoises. The fat of the abdominal region was present as thin, flat plates or disks of roundish form, 10 to 15 mm. in diameter, lodged in the peritoneum. The animal was a male."

In 1917 the body of a rattlesnake 159 cm. long (3.8 cm. of which represented the rattle), weighing 1939 grams, was peptonized at the American Museum of Natural History and the weight of skeleton thus prepared was found to be 205 grams. On the assumption that the skeleton was completely dry and that it was made up exclusively of mineral matter, it would represent 10.5 per cent of the flesh weight. This percentage does not, however, include the ash of the skin or of the flesh. Dr. Rand was impressed with the fact that the skeleton of the 1931 python was relatively light, which he thinks consistent with the fact that the body weight rests directly on the ground and there is free mobility of all parts. On the other hand, the high percentage of ash found in the total body of the 1931 python would suggest that the skeleton was rather large, unless there is a high percentage of ash in the flesh.

The chemistry of the body of snakes has been little studied. Kerr<sup>1</sup> reports an analysis of the fat content of a boa constrictor. The egg-shaped masses of fat spoken of by him are in full conformity with the buttons of fat noted when our 1931 python was dissected.

<sup>1</sup> Kerr, R. H., *Journ. Amer. Chem. Soc.*, 1927, **49**, p. 2046.



## GASEOUS METABOLISM AND ENERGY TRANSFORMATIONS OF THE FASTING SNAKE

### CARBON DIOXIDE AS A MEASURE OF HEAT PRODUCTION

Since the Nutrition Laboratory possesses calorimeters of various forms, it may be surprising that direct calorimetric measurements were not a prominent feature of this study. The earliest and, indeed, the most extensive use of direct calorimetry with cold-blooded animals was the study of Krehl and Soetbeer,<sup>1</sup> who employed a Rubner calorimeter. A personal visit to the laboratory of Hári in Budapest showed that as early as 1909 his differential compensation calorimeter<sup>2</sup> was being used in some preliminary observations on the heat production of a small crocodile. The results were never published. Hill<sup>3</sup> employed a differential calorimeter successfully in a study of cold-blooded animals. He found it made no difference whether pure oxygen or air was used in his calorimeter. With these methods of direct calorimetry it was usually necessary to immerse the animals in water or to study them exclusively in saturated atmospheres. For our experimental animals, this type of apparatus presented an abnormal condition of life. A few tests were made with our boa N and the 1931 python in the emission calorimeter of the Nutrition Laboratory (see pages 116 and 423), and important deductions were drawn therefrom, but our experience proved that it is out of the question to attempt to measure directly the heat production of these large terrestrial, cold-blooded animals. No matter how successful direct measurement of heat production may be with animals submerged in water, radiation or emission calorimeters are obviously useless for studying animals whose body temperature is actually somewhat below that of the environment. Gaseous metabolism measurements are therefore the best means of studying the energy transformations of cold-blooded animals. Although the measurement of a respiratory product, water vapor, has been considered in a preceding section of this report (see pages 114 to 130), the term "gaseous metabolism" is usually applied to the interchange of oxygen and carbon dioxide in the living organism. In order to secure an index of the energy transformations of these animals, our technique employed in the New York series of observations was so arranged that it was possible to measure accurately the carbon-dioxide production. But the determinations of the oxygen consumption were only partly successful.

Ideally, the determination of the oxygen consumption would be the best indirect measure of the heat production, for the caloric value of oxygen is practically unchanged with different respiratory quotients, the maximum difference being but 7 per cent, whether fat or carbohydrate is burned. Since snakes eat almost no carbohydrate, it was thought probable that the respiratory quotients would range only between the quotient of fat and that of protein. Between these limits the caloric value of carbon dioxide varies only about 10 per cent. With air-tight, closed-circuit respira-

<sup>1</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 611.

<sup>2</sup> Hári, P., *Abderhalden's Hand. d. biolog. Arbeitsmethoden*, 1925, Abt. IV, Teil 10, p. 711.

<sup>3</sup> Hill, A. V., *Journ. Physiol.*, 1911-1912, **43**, p. 261.

tion apparatus, such as were used in our New York series of experiments, it is impossible to lose or gain carbon dioxide. All the carbon dioxide produced is therefore collected and weighed, and the only probability of error is in the efficiency of the absorbing vessels and in the accuracy of weighing. Since it is possible to safeguard against these errors, the determination of the carbon-dioxide production in the closed circuit is extraordinarily accurate. The measurement of the oxygen consumption is much more complicated. With the closed-chamber technique employed in our New York series of experiments the measurement of the oxygen consumption required an exact knowledge of the *average* temperature of a relatively large volume of air, in part affected by the thermostatic control of the temperature of the respiration chamber and in part by the temperature of the room. Such measurement also demanded knowledge of the relative humidity, and the water content of the air in these closed chambers was difficult to control. The barometric pressure inside the system must likewise be known at the beginning and end of each period. But when small amounts of oxygen are consumed over periods lasting sometimes from 6 to 12 hours, as with these cold-blooded animals, gross fluctuations in pressure may be expected to occur in that time, and the determination of the oxygen consumption under such conditions presents infinitely greater difficulties than does the oxygen measurement in a short period with man.

Since in most of our experiments the cold-blooded animals that we studied were in the fasting condition, it was assumed that they were subsisting upon fat and that therefore the respiratory quotient would be about 0.72. Examination of the long series of quotients based upon the approximate measurements of oxygen consumption in the New York series of experiments and upon the exact oxygen determinations in the 1930 and 1931 series, when gas analysis was used, shows that, although there was considerable variability above and below this value, the average respiratory quotient of these animals in the fasting condition, whether snakes or tortoises, is close to 0.72. Hence in all our experiments, except the 1930 series with tortoises and the 1931 series with the python (see pages 206 and 386), we have made use of the carbon-dioxide measurements alone and have computed the fasting heat production therefrom by assuming the caloric value of carbon dioxide at the respiratory quotient of 0.72. The oxygen measurements thus became less vital in our New York series, and the carbon-dioxide measurements alone were considered significant.

Joel, in Kestner's laboratory, has criticized the use of carbon dioxide as a measure of heat production with cold-blooded animals.<sup>1</sup> He claims that the production of carbon dioxide and the absorption of oxygen are two separate processes and that the carbon-dioxide production can not be used as a measure of the heat production, but the oxygen consumption should be measured directly. Most of the curves published by Joel (all of them based on experiments with animals much smaller than rats) indicate an increase in oxygen consumption with increasing temperature, a more rapid effect of temperature as the temperature goes up and, in some cases, a decrease in oxygen consumption at the higher temperatures. There is no

<sup>1</sup> Joel, A., *Zeitschr. f. physiol. Chemie*, 1919, **107**, p. 233.

hint in any of our observations that there is an optimum point beyond which the oxygen consumption falls off rapidly, as is noted in some of Joel's experiments. Although our earlier determinations of oxygen were not at all satisfactory, the general picture obtained from the study of all our data shows that the respiratory quotient of our fasting animals remained close to 0.72. Further observations on cold-blooded animals in which accurate measurements of both the oxygen consumption and the carbon-dioxide production are obtained would certainly seem justifiable. Another point emphasized by Joel is that the partial pressure of oxygen influences oxygen consumption. Hill, on the other hand, found that the use of oxygen instead of air in his calorimeter made no measurable difference in the average heat production.<sup>1</sup> The evidence for this statement is not clear in Hill's paper. We avoided abnormally high percentages of oxygen in our observations and can state definitely that in general the oxygen content of the chamber air was essentially that of ordinary outdoor air. In all the experiments during 1930 and 1931 outdoor air only was used in the respiration chambers.

#### EFFECT OF AGITATION ON GASEOUS METABOLISM OF THE SNAKE

Early in our study (March 1916) it was noted that on two occasions after handling the large python its metabolism remained at a high level for a long time and only gradually settled down after about 5 hours to a reasonably constant value. On these two occasions girth measurements were made (fig. 40, p. 145), during which operation the python was handled by five men, and the snake struggled more or less. This high metabolism pointed clearly to an effect of agitation or muscular activity. At this time rectal temperature measurements following agitation had not been made; indeed, it was a year later before such measurements were carried out. As is shown in table 6 (p. 62), agitation resulted in a marked increase in rectal temperature. In one case at least the body temperature rose 6° C. within 35 minutes, with considerable agitation between each temperature reading. These rectal-temperature measurements were made on a boa, an animal notably much less irritable than the python. The metabolism measurements of the large python will be found in table 53 (p. 202). In the discussion of this table, as indeed in the discussion of many of the subsequent tables in which the metabolism of the various serpents is reported, one will continually find reference to periods of measurement preceded by agitation caused by handling, by placing the snake in its new environment, by body-temperature measurements, or by deliberate insult. In all cases an increased metabolism is noted.

In February 1917, a special series of experiments was planned to study with one serpent the course of the metabolism following periods of agitation. The snake used was the small Indian python, an animal that was the subject of many metabolism measurements at varying environmental temperatures. At this time the python weighed approximately 6 kg. and had been without food for from 9 to 19 days only. The results are shown in table 29. The animal was deliberately and severely insulted or agitated just prior to each experiment, but there were no indications of

<sup>1</sup> Hill, A. V., *Journ. Physiol.*, 1911-1912, **43**, p. 386.

definite muscular activity during the periods of gaseous metabolism measurement. By accident, before the first experiment on the first day, February 14, the snake escaped into the room and was consequently severely agitated just prior to the first period. Indeed, the agitation was much more intense than that preceding the second experiment on February 14.

TABLE 29—*Effect of agitation on metabolism of small Indian python*<sup>1</sup>

Date, weight, and days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environ- mental tempera- ture
	No.	Dura- tion		
		<i>mins.</i>	<i>gm.</i>	<i>°C.</i>
Feb. 14	1	38	6.222	31.3
6.09 kg.	2	40	3.783	30.4
9 days	3	40	2.365	29.9
	4	40	1.773	29.6
	5	40	1.478	29.2
	6	40	1.300	29.2
	7	40	1.123	29.6
Feb. 14	1	45	3.954	29.5
6.07 kg.	2	40	1.957	29.0
9 days	3	40	2.016	28.7
	4	40	1.127	28.8
Feb. 15	1	60	4.507	31.9
6.07 kg.	2	60	2.254	32.0
10 days	3	60	1.621	31.2
	4	65	1.752	31.2
	5	60	1.740	32.0
Feb. 16	1	60	5.316	36.4
6.05 kg.	2	90	2.354	36.8
11 days	3	68	2.240	37.8
	4	80	2.440	38.1
Feb. 23	1	60	2.488	23.3
5.98 kg.	2	64	1.580	24.2
18 days	3	60	1.324	23.9
	4	76	1.077	23.9
	5	61	1.105	24.1
	6	60	1.124	24.3
	7	52	1.065	24.3
Feb. 24	1	74	1.962	21.8
5.95 kg.	2	60	1.129	21.7
19 days	3	60	.928	21.7
	4	60	.807	21.9

<sup>1</sup> Deliberately and severely agitated just before each experiment.

The temperature of the environment was approximately 30° C. in both series. There was a pronouncedly high metabolism in the first period of the first series, with continually decreasing values in the subsequent periods. After seven 40-minute periods, the carbon-dioxide production per kilogram of body weight per 24 hours, at 30° C., was 1.123 grams. As will be seen from the detailed analysis of the data obtained with this small Indian

python (see pages 192 to 201), the metabolism of this particular animal at about this time had reached approximately its constant level at this environmental temperature (30° C.) and the effect of the previous disturbance had for the most part worn off at the end of the fourth period. In the second experiment on February 14, which was also preceded by agitation, a low level in metabolism was reached in the fourth period, the first three periods giving definitely high values. Prior to the second experiment the snake was agitated by being removed from the respiration chamber. It was out of the chamber about 7 minutes, unquestionably in a room temperature measurably below 30° C., which would tend to lower its metabolism.

On February 15 the python was again agitated just before the experiment, and high metabolism values are noted for the first two periods at least. The average value of 1.7 grams is probably not far from the normal carbon-dioxide production of this snake per kilogram of body weight per 24 hours at the high environmental temperature that prevailed. On February 16 the environmental temperature was much higher than in the preceding experiments, but in spite of this fact there was a high carbon-dioxide production in the first period. At the end of 60 minutes probably the effect of agitation had worn off, since the animal was already at a high metabolic level due to the high environmental temperature. The snake was about ready to shed on February 16, and it was thought best not to use it the next day. As late as February 21 it had not actually shed its skin. On February 23 an experiment was carried out at a much lower temperature. Here the after-effect of agitation continued a little over 3 hours. In all instances, except on February 24, the temperature of the room in which the python was agitated was considerably lower than the temperature of the respiration chamber in which the carbon-dioxide production was measured. On February 24 the room temperature was essentially the same as the chamber temperature. The high carbon-dioxide production in the first period on this day is therefore due more specifically to agitation, uncomplicated by the depressing effect of a cooler environment.

The effect of agitation was also noted in experiments with boa N, as has already been pointed out in the discussion of water vapor (p. 121). On February 18 and 19, 1920, at an environmental temperature of 35° to 36° C., the carbon-dioxide production per kilogram of body weight per 24 hours of this boa, while quiet, fasting, without any transition in environmental temperature, and unaffected by handling or agitation, averaged 1.61 grams. On February 20 at 23° C. the carbon-dioxide production immediately following a period of handling for body-temperature and body-surface measurements was 1.88 grams. Thus, although the environmental temperature in the February 20 experiment was 13° lower, the carbon-dioxide production was greater than in the two preceding experiments at the higher temperature, due to the agitation.

The general picture from these data is that after agitation there is a pronounced increase in metabolism, measured always during periods devoid of muscular activity, in some instances four- or nearly six-fold. The

higher the environmental temperature, the more quickly the effect of agitation wears off. From the practical standpoint, therefore, it is necessary that the preliminary period prior to any metabolism measurements made to study the influence of some particular factor, should always be sufficiently long to insure the disappearance of any effect due to agitation. The nature of this increased metabolism is of considerable interest. It may be caused by muscular activity *per se*, due to the struggle and agitation. It may be the result of a normal increase in cell activity due to an increased temperature. Finally, it is conceivable that the irritation of the snake may correspond to the psychic stimulus noted with humans. It is evident that as a result of agitation there is a profound increase in rectal temperature accompanied by an increase in metabolism. It therefore seems probable that this increase in metabolism is due to both factors, the actual muscular effort itself, which results in increased heat production, and the after-effect of muscular activity, during which period the previously warmed cells are slowly cooling off but maintaining a metabolism higher than normal. A more striking illustration could hardly be found of the individuality of the cold-blooded animal in regulating its body temperature rapidly. Contrary to the experience of humans or warm-blooded animals, the heat produced by the muscular activity of the snake, instead of being disengaged and liberated, is stored, resulting in a relatively great increase in body temperature. This in turn raises the temperature of the cells, which likewise results in a stimulated metabolic activity. It is believed that this reaction of the cold-blooded animals to muscular activity and agitation has a most important bearing upon the differences in the mechanism of heat loss between the so-called "warm-blooded" and "cold-blooded" animals.

#### STANDARD METABOLISM OF SNAKES

In order to compare the metabolism of the same animal or of different animals at different environmental temperatures and at different stages of fasting, it is necessary that the conditions of measurement should be the same in every experiment except for the particular factor being studied. With cold-blooded animals conditions comparable to those considered prerequisite in measuring the basal metabolism of humans can not be obtained. The human will voluntarily abstain from eating in order to reach the post-absorptive state, and his metabolism is practically unaffected by changes in environmental temperature within reasonable limits. But the cold-blooded animal can not cooperate in securing the post-absorptive state, although prolonged fasting is easily secured, and its metabolism is extremely sensitive to changes in environmental temperature. Our metabolism measurements made for comparative purposes on large snakes were therefore carried out under conditions that, although not strictly basal, approximated in so far as possible basal conditions with humans. These measurements will be spoken of as "standard metabolism measurements." In the first place, the standard measurements were made only when the snake had been at least five days<sup>1</sup> without food. In the second place, only

<sup>1</sup> See digestion experiments with snakes, pp. 247 *et seq.*

periods without activity, when the snakes were quiet, were considered. The problem of activity is a serious one with warm-blooded animals but with cold-blooded animals, such as snakes, this problem hardly enters, although at times one will see in the results the influence of activity. In the third place, only those periods unaffected by previous agitation were accepted. As has already been shown, the agitation of the snake results in increased muscular activity at the time of agitation and in a high body temperature; and in the subsequent experimental periods, though the snake is in muscular repose, there will be a greater output of water vapor and an increased carbon-dioxide production. For comparative purposes the metabolism of snakes should not be measured too soon after handling or transference from one place to another. The environmental temperature should be constant, not only during the actual period of measurement but likewise for some time prior to the period of measurement. In some instances, as will be seen in subsequent tables, one can note definitely the effect of transition in environmental temperature when the snake was transferred from a low to a high temperature and *vice versa*. Only those values, however, obtained during periods when the environmental temperature remained constant for some time may be considered as comparable or of use in studying the effect of body or of environmental temperature upon the gaseous metabolism of the snake.

To make the picture complete, the rectal temperature of the snake should have been determined simultaneously with the measurement of the standard gaseous metabolism but, as is clearly seen, any factor causing irritation or agitation of the snake itself raises the metabolism. Hence the simultaneous determination of rectal temperature would have defeated the object of the comparative measurements. There is no doubt, however, that the markedly increased rectal temperature invariably found as a result of agitation with boas I and D on July 3 to 6, 1917 (table 6, p. 62) reflects what would have happened to the rectal temperatures of our other snakes, had the body temperature been determined during each period when the gaseous metabolism was being measured. When the body temperature was determined, it was always done at the end of the experiment.

The standard metabolism measurements were carried out in the respiration chamber according to the techniques described on pages 17 to 42. The length of the period varied with the size of the snake and particularly with the special factor under study. The general rule in the New York series was to conduct the experiment a sufficient length of time to collect in the absorbing vessels at least one gram of carbon dioxide, in order to minimize any slight error that might occur in the weighing of the rather large recipients. The standard heat production for all except the 1930 tortoises and the 1931 python was computed by multiplying the standard carbon-dioxide production by the caloric value of carbon dioxide at an assumed respiratory quotient of 0.72.<sup>1</sup> The values for the standard carbon-dioxide production are reported in the following tables for each individual period, but the values for the standard heat production are averages, based

<sup>1</sup> See page 151.

upon the average standard carbon-dioxide production for the given date. In the case of the 1930 tortoises and the 1931 python, the heat production was computed from the measured oxygen consumption and the actually determined respiratory quotient.

It will be noted that in the tables in which the standard carbon-dioxide production and oxygen consumption are reported, periods have frequently been included that were obviously complicated by agitation. These are usually the first periods of the series, that is, those following body-temperature measurements, surface-area measurements, or mere handling in removing the snake from its den or cage and placing it in the respiration chamber. Periods affected by transitions in environmental temperature or by muscular activity of the snake have likewise been included. To distinguish between these periods and those unaffected by these factors, an asterisk has been placed against the values representing the "standard metabolism," and these starred values alone will be used in our discussion of the standard metabolism of the same animal and in all comparisons of the standard metabolism of different animals at different environmental temperatures. In every instance the first period of each experiment was preceded by a preliminary period of measurement varying in length from a few minutes to an hour or over. The values for body weight enclosed in parentheses were not actually determined but assumed from body weights obtained on some other day very near the given date.

#### STANDARD METABOLISM OF BOA A

On account of their irritability and relatively high cost the pythons could not be extensively studied, but the boas were much more placid and could be replaced at a not prohibitive cost in case of death. The metabolism of 14 boa constrictors (boas A to N) ranging in weight from 4 to 13 kg., was studied under considerable differences in environmental temperature. With boas A, B and C the program called for but one experimental period a day, ranging in length from 4 to 27 hours. This depended upon the probable carbon-dioxide production, for at the high environmental temperatures shorter experiments could be made. There were, however, no second periods for comparison on any individual day. Hence we are dealing in these three cases with one measurement for the given date, made at one environmental temperature.

The results of the standard metabolism measurements on boa A are given in table 30. Each carbon-dioxide and heat value in this table is considered to represent the standard metabolism. Although the experiments with boa A form one of our earliest series of measurements, in which the niceties of technique in handling and particularly the precautions regarding uniformity in environmental temperature were not fully appreciated, we believe in the approximate accuracy of these figures. There was at least no obvious reason for rejecting any of the results.

The length of time that this snake had gone without food prior to our first test was unknown. Probably it had been fasting but a few days. Before the preliminary period on November 3 began, it had been in the chamber some time. Boa A was fed in the middle of December and there-



after fasted for about two and one-half months, during which time its standard metabolism was determined in a series of experiments extending from January 3 to March 1, 1916. At the latter date it had been 75 days without food. During this period the body weight fell from 10.45 kg. on December 23, when it had been fasting 7 days, to 9.53 kg., a fall of 9 per cent. Regularity in the loss of body weight from day to day was not observed, for undoubtedly at times the snake took water. Boa A began getting ready to shed its skin about January 11, 1916. Its eyes began to clear on January 25 and its skin was shed on January 31.

TABLE 30—*Standard metabolism of boa A*

Date	Body weight	Days fast-ing	Length of period	CO <sub>2</sub> per kg. per 24 hours*	Heat produced per 24 hours		Environ-mental tempera-ture
					Per kg.*	Per sq.m.*	
1915	kg.		hrs.	gm.	cal.	cal.	°C.
Oct. 28.....	(10.23)	?	6	0.316	1.05	18.2	22.0
Oct. 29.....	(10.23)	?	6	.342	1.14	19.8	21.0
Nov. 3.....	10.23	?	4	.826	2.75	47.7	28.5
Nov. 4.....	(10.23)	?	4	.816	2.72	47.2	35.0
1916							
Jan. 3.....	10.00	18	9	.728	2.43	41.9	29.3
Jan. 4.....	10.00	19	12	.310	1.03	17.8	20.0
Jan. 10-11.....	10.00	25	21	.355	1.18	20.3	21.5
Jan. 11-12.....	(9.99)	26	27	.154	0.51	8.8	16.0
Jan. 13.....	(9.96)	28	11	.676	2.25	38.7	31.1
Jan. 17.....	9.90	32	10	.785	2.62	44.7	30.2
Jan. 19-20.....	9.84	34	15	.440	1.47	25.4	21.1
Jan. 21-22.....	9.90	36	17	.430	1.43	24.4	21.1
Jan. 22-23.....	9.84	37	20	.385	1.28	22.1	20.2
Jan. 24-25.....	9.84	39	17	.461	1.54	26.6	20.7
Jan. 27-28.....	9.84	42	14	.176	0.59	10.2	17.0
Feb. 3-4.....	9.67	49	20	.588	1.96	33.3	28.6
Feb. 9-10.....	9.64	55	21	.263	0.88	15.1	21.3
Feb. 10-11.....	9.64	56	17	.728	2.43	41.8	35.3
Feb. 15-16.....	9.64	61	17	.761	2.54	43.7	35.5
Feb. 19-20.....	9.55	65	23	.285	0.95	16.2	20.9
Feb. 23-24.....	9.55	69	20	.225	0.75	12.8	21.1
Feb. 26-27.....	9.55	72	16	.122	0.41	7.0	16.1
Feb. 28-29.....	9.55	74	15	.395	1.32	22.5	24.3
Feb. 29-Mar. 1..	9.53	75	15	.397	1.32	22.5	24.0

\* All values in this column represent standard metabolism.

Inspection of table 30 shows that in general the higher metabolism prevailed at the high environmental temperatures. But a close analysis of the relationship between environmental temperature and the standard metabolism is best made by considering figure 41. In this figure the heat production per kilogram of body weight per 24 hours (computed from the carbon-dioxide production by the method explained on page 156) has been referred to the environmental temperature. The values per unit of surface area will be discussed subsequently (p. 225). The trend of the standard heat production of boa A from 16° to 30° C. can certainly best be expressed by a straight line and, strikingly enough, the metabolism at 35°

and above is essentially the same as that at 30° C. Some points lie above this curve. That at 28.5° and that at 35° C. represent two of the first four experiments between October 28 and November 4, when the length of fasting was unknown. Since these two points lie above the curve, it is probable that boa A was not in a state of prolonged fasting at this time.

The metabolic plateau indicated between 30° and 35° with boa A is in conformity with scattered observations in the literature, notably those of Vernon,<sup>1</sup> although his subsequent experiments threw much doubt upon the existence of such a plateau. Although figure 41 gives reasonably good evidence of a fairly constant metabolic level, this finding is distinctly an exception to the results obtained with most of our other animals.<sup>2</sup> Obviously on a curve of this kind one can see that the calculation of the van't Hoff constant (see page 435) will vary considerably, depending at which temperatures the differences in metabolism are noted.

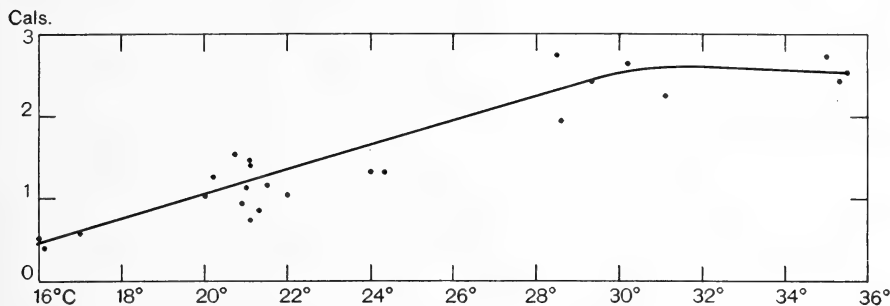


FIG. 41—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—BOA A.

#### STANDARD METABOLISM OF BOA B

This boa was of a different family from that of the other boas, inasmuch as it was a so-called "Cuban boa" (p. 7). With this boa (see table 31) the experiments covered essentially a month, from March 2 to April 7, 1916, and during this period the animal took no food. It had eaten a pigeon on January 26 and two pigeons on February 10, 1916, and had been fasting 21 days when the series of observations with it began. The initial weight of 12.90 kg. fell to 11.82 kg., a loss of 8 per cent. One or two incidents noted with boa B during the experiments implied that it was slightly more irritable than boa A, studied at about this same time, for simply raising the blanket spread over the respiration chamber to read the thermometer on the snake's box seemingly disturbed it somewhat. Each experiment consisted of a single period, preceded by a preliminary period. The length of each experiment ranged from 6 to 22 hours. On the morning of March 1 boa B shed its skin. It had commenced to shed on February 28. Following the experiments of March 28, April 3-4 and April 4-5 excreta were found in the snake's box.

<sup>1</sup> Vernon, H. M., *Journ. Physiol.*, 1894-95, **17**, p. 277; *ibid.*, *Journ. Physiol.*, 1897, **21**, p. 443.

<sup>2</sup> Evidence of a plateau in metabolism was also noted with a python. (See page 206.)

The temperature of the environment did not exceed 31.2° and was not maintained below 21.5°. As usually is the case, one notes the higher carbon-dioxide excretion per kilogram of body weight per 24 hours with the

TABLE 31—Standard metabolism of Cuban boa B

Date	Body weight	Days fast-ing	Length of period	CO <sub>2</sub> per kg. per 24 hours*	Heat produced per 24 hours		Environ-mental tempera-ture
					Per kg.*	Per sq.m.*	
1916	kg.		hrs.	gm.	cal.	cal.	°C.
Mar. 2-3.....	12.90	21	19	0.966	3.22	60.2	28.0
Mar. 3-4.....	12.87	22	15	1.093	3.64	67.9	27.5
Mar. 4-5.....	12.87	23	13	.730	2.43	45.3	24.5
Mar. 6-7.....	12.84	25	17	1.054	3.51	66.3	30.0
Mar. 7.....	12.84	26	9	1.147	3.82	72.1	30.5
Mar. 8-9.....	12.81	27	18	.493	1.64	30.9	21.5
Mar. 9-10.....	12.81	28	16	.498	1.66	31.3	21.5
Mar. 28.....	12.16	47	10	.645	2.15	39.6	27.1
Mar. 29.....	12.11	48	11	.766	2.55	46.8	27.5
Mar. 30.....	12.11	49	12	.797	2.66	48.8	27.3
Mar. 31.....	12.08	50	11	1.007	3.36	61.5	31.2
Apr. 1.....	12.02	51	9	1.016	3.39	61.7	30.4
Apr. 3-4.....	11.96	53	22	.416	1.39	25.6	21.6
Apr. 4-5.....	11.91	54	21	.409	1.36	24.9	21.6
Apr. 5-6.....	11.91	55	12	.813	2.71	49.7	27.5
Apr. 6.....	11.91	56	7	.856	2.85	52.2	27.9
Apr. 7.....	11.82	57	6	.678	2.26	41.1	28.0

\* All values in this column represent standard metabolism.

higher environmental temperature. The best indication, however, of the reaction of the metabolism to environmental temperature is seen in figure 42, in which the calories per kilogram of body weight per 24 hours are re-

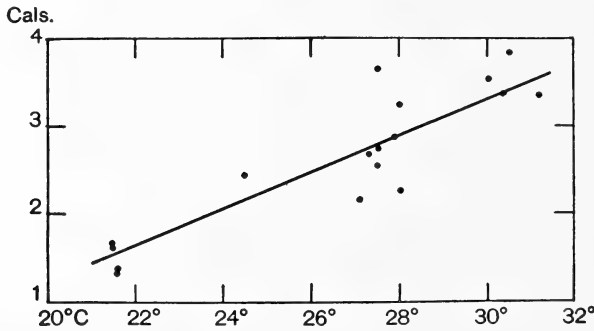


FIG. 42—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—Boa B.

ferred to the temperature of the environment. With this series of observations again one finds that the curve as drawn through these points would be a straight line and not a curve. If it is admitted that this straight line represents the probable trend of the standard metabolism, the heat

production at the different environmental temperatures can be compared and the effect of temperature noted. Thus, at 21°C. the average heat production would be 1.45 calories and at 31°C., 3.5 calories or 240 per cent greater.

#### STANDARD METABOLISM OF BOA C

Boa C was of essentially the same body weight as boa B and slightly heavier than boa A. Standard metabolism measurements (table 32) were made on it between May 23 and July 27, 1916, and it ate no food throughout the entire series of experiments. The boa was purchased for the Park about May 1, 1916, and it was assumed not to have eaten for 30 days at the time of the first experiment on May 23. The actual length of fasting is not known, but the general state of nutrition of boa C was such as to lead us to believe that it had not previously undergone any considerable period of fasting. The body weight changed in the 66 days of experimentation from 12.45 to 11.88 kg., a relatively small loss of only 4.6 per cent. On the morning of May 30 the boa's eyes were blue and, to aid in the shedding, it was sprinkled with water. On June 1 its eyes seemed their ordinary color. Its skin was torn a little when it was put into the

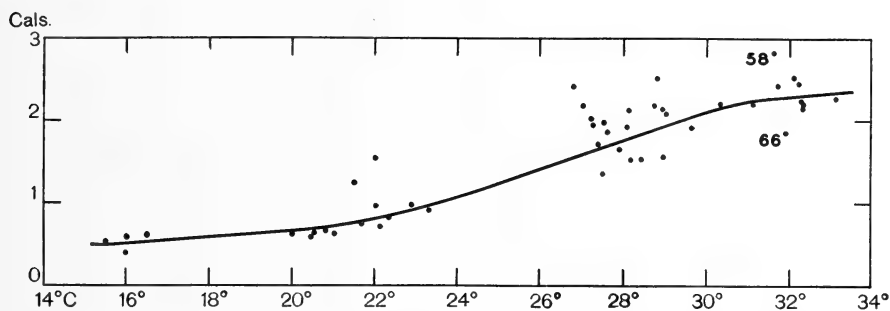


FIG. 43—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—BOA C.

Figures 58 and 66 against two of the plotted points indicate number of days snake had been fasting when these metabolism measurements were made.

chamber on June 4 and the boa shed its skin during the experiment of June 8-9.

It was impracticable to run experiments at a very high temperature with boa C, owing to its cost and the possible danger of losing it. Hence the highest temperature was 33.1° and the lowest 15.5° C. The standard metabolism, as in the other cases thus far examined, is characteristic in that it is high at the high temperatures and low at the low temperatures. The heat production, computed from the standard carbon-dioxide production, is plotted with reference to the environmental temperature in figure 43. With boa C the most probable course of the metabolism is not represented by a straight line but by a distinctly bowed line, such as is sketched on the chart, although this line takes the nature of a compound curve. The tendency for the metabolism to increase with increasing temperatures seems to stop at about 30°.

The days of fasting indicated in table 32 bring out the fact that, in general, at the same temperature the longer the fast the lower is the

TABLE 32—Standard metabolism of *boa C*

Date	Body weight	Days fasting	Length of period	CO <sub>2</sub> per kg. per 24 hours*	Heat produced per 24 hours		Environmental temperature
					Per kg.*	Per sq.m.*	
1916	kg.		hrs.	gm.	cal.	cal.	°C.
May 23.....	12.45	30	4	0.657	2.19	40.7	28.7
May 24.....		31	6	.639	2.13	39.6	28.9
May 25.....		32	7	.570	1.90	35.3	29.6
May 26.....		33	7	.660	2.20	40.9	30.3
May 27.....		34	7	.750	2.50	46.5	28.8
May 29-30.....		36	20	.723	2.41	44.8	26.8
May 31-June 1... <sup>1</sup> (12.39)		38	22	.651	2.17	40.3	27.0
June 1-2.....		39	24	.463	1.54	28.6	22.0
June 2-3.....		40	23	.376	1.25	23.1	21.5
June 5-6.....	(12.33)	43	21	.186	.62	11.4	16.5
June 6-7.....	(12.27)	44	26	.181	.60	11.0	16.0
June 7-8.....	(12.21)	45	18	.297	.99	18.3	22.0
June 8-9.....	(12.15)	46	18	.632	2.11	38.8	28.1
June 9-10.....	(12.09)	47	23	.603	2.01	36.8	27.2
June 12-13.....	11.99	50	18	.217	.72	13.3	22.1
June 13-14.....		51	20	.163	.54	10.0	15.5
June 14-15.....		52	20	.119	.40	7.4	16.0
June 15-16.....		53	20	.277	.92	16.9	23.3
June 16-17.....		54	18	.756	2.52	46.4	32.1
June 19-20.....	11.96	57	17	.738	2.46	45.3	32.2
June 20-21.....		58	19	.851	2.84	52.3	31.6
June 21-22.....		59	20	.564	1.88	34.6	27.6
June 22-23.....		60	20	.496	1.65	30.4	27.9
June 23-24.....		61	20	.294	.98	18.0	22.9
June 26-27.....	12.13	64	15	.244	.81	14.9	22.3
June 27-28.....		65	22	.458	1.53	28.1	28.2
June 28.....	(12.12)	66	10	.557	1.86	34.2	31.9
June 29-30.....	(12.11)	67	20	.659	2.20	40.4	32.3
June 30-July 1... (12.10)		68	21	.571	1.90	34.8	28.1
July 3-4.....	(12.06)	71	20	.205	.68	12.4	20.8
July 5-6.....	(12.01)	73	19	.227	.76	14.0	21.7
July 6-7.....	(11.98)	74	20	.458	1.53	28.2	28.4
July 7-8.....	(11.96)	75	21	.662	2.21	40.7	31.1
July 10-11.....	11.91	78	20	.688	2.29	42.0	33.1
July 11-12.....	(11.88)	79	21	.629	2.10	38.4	29.0
July 12-13.....	(11.87)	80	21	.585	1.95	35.6	27.3
July 13-14.....	(11.86)	81	19	.185	.62	11.3	20.5
July 14-15.....	(11.85)	82	20	.186	.62	11.3	20.0
July 17-18.....	11.82	85	12	.472	1.57	28.5	28.9
July 18-19.....		86	20	.511	1.70	30.9	27.4
July 19-20.....		87	20	.665	2.22	40.4	32.3
July 20-21.....		88	20	.728	2.43	44.2	31.7
July 21-22.....		89	17	.593	1.98	36.0	27.5
July 24-25.....	(11.96)	92	20	.188	.63	11.6	21.0
July 25-26.....	(11.93)	93	20	.183	.61	11.2	20.5
July 26-27.....	(11.91)	94	20	.407	1.36	24.9	27.5
July 27.....	11.88	95	6	.653	2.18	39.8	32.3

\* All values in this column represent standard metabolism.

<sup>1</sup>Weight obtained on June 4.

metabolism, although this is by no means invariably the case. A preponderance of the values obtained during the longer periods of fasting lie below the curve in figure 43. Wide deviations from the general trend are to be noted, particularly in the results for the thirty-fourth to the fortieth day of fasting. Here perhaps is, for the first time in our study,

a suggestion as to the effect of shedding on metabolism, for on precisely these days, according to our protocols, was the shedding period of this animal. We have no explanation for the high value on the fifty-eighth day of fasting or for the exceptionally low value on the sixty-sixth day. The data for the shedding period are too scanty thus far to permit drawing any general conclusions, but certainly one is justified in inferring from the results on this particular boa that shedding is not without influence upon metabolism. This influence would be quite in line with the general impression of the curators of reptiles in various parks, who consider shedding one of the most important physiological phases of the snake's existence.

#### STANDARD METABOLISM OF BOA D

Boa D was one of the larger snakes, with an initial weight of 12.96 kg. The animal arrived at the New York Zoological Park on March 8, 1917, and was assumed not to have fed for thirty days before its arrival. It is quite within the bounds of possibility, however, that it had been without food since its capture in South America, an unknown period of time, although the state of nutrition was not bad. Two series of experiments were made with boa D, the first from March 15 to July 6, 1917. The research at the New York Zoological Park was then discontinued for eight or nine months, and the second series with this animal began April 5 and ended June 29, 1918. The observations with boa D differed from those with boas A, B and C, in that each experiment comprised a number of periods. The variation in metabolism from period to period can therefore be studied. The periods were from 2 to 14 hours in length, depending upon the environmental temperature and the amount of carbon dioxide produced. The snake was fasting in all experiments.

In table 33 are recorded the pertinent data for boa D. Those particular carbon-dioxide values have been starred that can be considered as obtained under standard conditions, that is, for use for comparative purposes uncontaminated by excessive activity, agitation, inadequate temperature adjustments, or food. The uniformity of the metabolism of boa D from period to period is strikingly shown on a number of dates, for example, on June 27 to 29, when there were seven consecutive periods at a high temperature. At the low temperature on March 15 to 17, averaging 18.2° C., there are also five well-agreeing periods. Indeed, throughout the entire table one sees evidence of uniformity in the metabolism, speaking both for uniformity of technique and for regularity in the physiological processes of the animal.

On March 24, 1917, boa D was about to shed. The skin was shed on either April 1 or 2. Rectal temperature observations were secured at the end of several of the experiments, as follows:

Date	Rectal temp (°C.)	Respiration chamber temp. (°C.)
June 9, 1917	27.80	27.57
June 26, 1917	25.65	25.89
July 6, 1917	28.00	27.83
April 6, 1918	31.37	32.34
June 29, 1918	29.27	29.07

TABLE 33—*Metabolism of boa D—Fasting*

Date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1917			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Mar. 15	37 days	1	8	*0.283	19.3
Mar. 15-16	12.96 kg.	2	14	*.294	18.5
Mar. 16		3	8	*.284	17.8
Mar. 16-17	12.92 kg.	4	10	*.326	17.6
Mar. 17		5	10	*.252	17.7
Mar. 19 <sup>1</sup>	41 days	1	8	*.634	23.6
Mar. 19-20	12.87 kg.	2	6	*.626	23.2
Mar. 20		3	6	*.546	23.1
Mar. 20	12.85 kg.	4	7	*.598	23.3
Mar. 20-21		5	7	*.573	23.3
Mar. 21		6	8	*.553	23.4
Mar. 21	12.85 kg.	7	7	*.614	23.2
Mar. 22	44 days	1	3	*1.520	30.3
Mar. 22	12.79 kg.	2	2	*1.434	29.9
Mar. 22		3	3	*1.298	29.4
Mar. 22 <sup>2</sup>		4	4	*1.126	29.3
Mar. 23	45 days	1	3	*1.227	30.0
Mar. 23	12.70 kg.	2	3	*1.299	29.9
Mar. 23		3	3	*1.439	29.8
Mar. 23		4	3	*1.134	29.6
Mar. 24	46 days	1	4	*1.098	29.7
Mar. 24	12.61 kg.	2	3	*1.288	29.8
Apr. 5 <sup>3</sup>	58 days	1	3	*.532	27.9
Apr. 5	12.93 kg.	2	4	*.603	27.6
Apr. 5		3	4	*.594	28.0
Apr. 5-6		4	8	*.627	28.3
Apr. 6		5	6	.873	28.3
Apr. 20	73 days	1	3	*.575	30.2
Apr. 20	12.77 kg.	2	6	*.603	30.5
Apr. 20-21		3	8	*.718	30.4
Apr. 21		4	7	*.679	30.5
Apr. 21 <sup>4</sup>		5	6	*.698	30.9
Apr. 23	76 days	1	4	.815	33.6
Apr. 23	12.64 kg.	2	4	.679	31.7
Apr. 23		3	4	.916	30.3
Apr. 23-24		4	5	*.696	29.3
Apr. 24		5	5	*.639	28.8
Apr. 24		6	5	*.634	28.4
Apr. 24		7	6	*.575	28.4
June 7	121 days	1	7	*.676	29.0
June 7-8	12.34 kg.	2	11	*.575	28.3
June 8		3	8	*.675	29.0
June 8		4	6	*.581	28.5
June 8-9		5	6	*.652	28.0
June 9	12.32 kg.	6	7	*.638	27.8

TABLE 33—*Metabolism of boa D—Fasting (Continued)*

Date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1917			hrs.	gm.	°C.
June 23-24	137 days	1	5	* .784	29.4
June 24	12.45 kg.	2	7	* .622	28.9
June 24		3	6	* .585	29.1
June 24	12.43 kg.	4	5	* .713	30.1
June 24		5	5	* .788	29.8
June 25		6	6	* .669	28.9
June 25	12.43 kg.	7	6	* .483	28.4
July 5	149 days	1	6	* .631	29.9
July 5-6	12.12 kg.	2	7	* .528	29.9
July 6		3	10	* .640	28.8
July 6		4	6	* .575	27.9
1918					
Apr. 5 <sup>b</sup>	1 year,	1	5	.700	28.2
Apr. 5	58 days	2	8	*1.012	31.3
Apr. 5-6	8.16 kg.	3	11	*1.120	32.4
Apr. 6		4	7	*1.429	32.3
June 27	1 year,	1	3	*1.280	31.3
June 27	141 days	2	7	*1.248	30.9
June 27-28	6.69 kg.	3	8	*1.274	30.4
June 28		4	8	*1.300	29.7
June 28		5	8	*1.176	29.4
June 28-29		6	9	*1.260	29.3
June 29		7	8	*1.159	29.2

\* Only starred values represent standard metabolism.

<sup>1</sup> Taken from room at 17° C. and put in chamber at 23° C. about 1 hr. 30 min. before period 1.

<sup>2</sup> Cover taken off chamber for night at 11 p.m.

<sup>3</sup> Boa put into chamber on Apr. 4 to remain overnight.

<sup>4</sup> Boa not returned to reptile house, Apr. 21, but remained in chamber over Apr. 22.

<sup>5</sup> Boa in chamber overnight, Apr. 4-5, 1918, but apparently was not at as high temperature as on Apr. 5-6. Temperature in period 1 is in doubt, because of sharp rise in first 2 hrs., without intermediate observations.

In table 33, as in the preceding tables, one notes the effects of some of the factors influencing metabolism, notably a sluggishness in temperature adjustment. Thus, on April 23 in the first three periods the carbon-dioxide production was higher than in the following periods, because the temperature of the environment, although steadily falling, was higher. On the other hand, in the experiment of April 5-6, 1918, the metabolism in the first period was lower than in the subsequent periods because the temperature was rising and the snake had not yet adjusted itself. Another carbon-dioxide value in the table not starred and not considered standard (0.873 gram) is that for the fifth period in the experiment of April 5-6, 1917. This is a noticeably higher value than any preceding it. We have no explanation for it. Activity records unfortunately were not obtained on this particular day, but boa D rarely showed any activity.



The body weight of boa D steadily decreased from March 15, 1917, when it was 12.96 kg., to the end of the experimentation that year, July 5, when it was 12.12 kg. This represents a loss of 6.5 per cent in 112 days. A considerable length of time then elapsed before boa D was used again, and unfortunately there exists an element of uncertainty about the feeding of this animal when the experimental series was resumed on April 5, 1918. Mr. Snyder, who at that time was in charge of feeding the snakes in the New York Zoological Park, was doubtful whether boa D had eaten once in July 1917, or whether it had been on an absolute fast since it was brought to the reptile house from the dealer. In these calculations it has been assumed that no food was taken in July 1917. The condition of the snake showed an obviously bad state of nutrition. In our protocols are fre-

TABLE 34—*Standard heat production of boa D*

Date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq.m.	
1917-1918		<i>cal.s.</i>	<i>cal.s.</i>	°C.
Mar. 15-17	37	0.96	18.0	18.2
Mar. 19-21	41	1.97	36.7	23.3
Apr. 5	58	1.96	36.7	28.0
June 7-9	121	2.11	38.8	28.4
Apr. 23-24	76	2.12	39.4	28.7
July 5-6	149	1.98	36.4	29.1
June 23-25	137	2.21	41.0	29.2
Mar. 22	44	4.48	84.3	29.7
Mar. 23	45	4.25	79.4	29.8
Mar. 24	46	3.98	73.8	29.8
June 27-29	1 year, 141 days	4.14	62.9	30.0
Apr. 20-21	73	2.18	40.9	30.5
Apr. 5-6	1 year, 58 days	3.95	63.2	32.0

<sup>1</sup> Derived from starred data in table 33.

quent records as to the condition of boa D, such as that on April 5, 1918, namely, "The animal has lost a great deal of weight; its skin hangs loosely on its bones, and its body feels as if there is no flesh present. For months it was thought that this boa was about to die." On June 27, 1918, it was recorded that the boa was "nothing but skin and bones." It was not in a condition to be handled, as the skin on the hide easily became disengaged from the flesh in large patches. All these records indicate that the snake was in the last stages of emaciation. Boa D died July 12, 1918, or 13 days after the last experiment.

Inspection of the data in table 33 shows, as has been commonly the case thus far, that the low metabolism is usually coincidental with a low environmental temperature. There are, however, instances where a high metabolism is found at a temperature not appreciably higher than that in other experiments where the metabolism is lower. Thus, if one compares the data for June 23 through July 6, at a temperature of essentially

30° with the data for June 27 to 29, at the same temperature, one sees that there is an enormously increased metabolism per kilogram of body weight in the latter case. Boa D in this second instance had lost nearly half its initial weight, after a fast of presumably 1 year and 141 days.

In an attempt to study more carefully the relationship between the metabolism and the environmental temperature, we have recorded in table 34 and plotted in figure 44 the 24-hour heat production per kilogram of body weight referred to environmental temperature. The distribution of the plotted points in this chart is such as to make an analysis of the data difficult, if not, indeed, impossible. Here there is no hint of regularity in the course of the metabolism with increasing temperature. Unfortunately only two measurements were made below 28°. At about 30° there is the seemingly impossible situation of three well-agreeing experiments on the forty-fourth, forty-fifth and forty-sixth days of fasting showing values of about 4.0 or 4.5 calories, and another experiment on the seventy-third day of fasting showing, at the same temperature, a much lower metabolism. Nearly a year later, when boa D had been fasting 1 year and 141 days and when its body weight was about half of the initial body weight, the metabolism was extraordinarily high. In other words, at a temperature of 30° boa D had the same metabolism per kilogram of body weight when it weighed 6.69 kg. and had been fasting 1 year and 141 days, as it did when it weighed 12.7 kg., and had been fasting only 45 days. This high metabolism following prolonged fasting is further confirmed by measurements made on April 5-6, 1918, when boa D had been fasting 1 year and 58 days. In this experiment, at an average temperature of 32°, a high metabolism was found, although a little lower than that noted on June 27-29.

We have hesitated to draw any curve in figure 44. From the large number of standard heat-production values obtained with boa D, each the average of from 2 to 7 well-agreeing periods, it was expected that the course of the metabolism would be unusually well established. The picture is not made any clearer, even if one questions and excludes the two points at over one year's fasting, on the ground that we may have been dealing with an entirely different animal at this time. Our 9-months' absence from the Park, the impossibility of controlling the individuality of all the snakes in the Park, and the difficulties of selecting nearly a year later precisely the same boa that had previously been studied may throw doubt upon the identity of this snake.

The three high values at 44, 45 and 46 days of fasting are so at variance with the values at 58 to 149 days at about the same temperature that a satisfactory explanation is difficult. If the values at 37 and 41 days, that is, at 18.2° and 23.3°, are correct, one would expect a metabolism at 30° not far from that represented by the values at 44, 45 and 46 days, and one would not expect to find the same metabolism at 23° when the snake had been 41 days without food as at 29°, when the snake had been fasting 149 days. Assuming for the moment that the values at 44, 45 and 46 days are abnormally high, we have perhaps an explanation for the high metabolism in the fact that at the close of these tests two ticks were found on boa D. The discomfort caused by these parasites is well known to snake handlers.

It is not unlikely that even at 23° the value is higher than it would have been if the ticks had not been on the snake. If one makes allowance for the irritation of these parasites, a curve might be drawn that would lie much lower than these points under discussion and would pass through the points grouped around 2.0 calories at about 29°. But there still remain the extraordinarily high values for the fasting period of over one year. No matter from what standpoint one looks at figure 44, it is impossible to conceive of any relationship between the metabolism per unit of weight and the temperature of the environment.

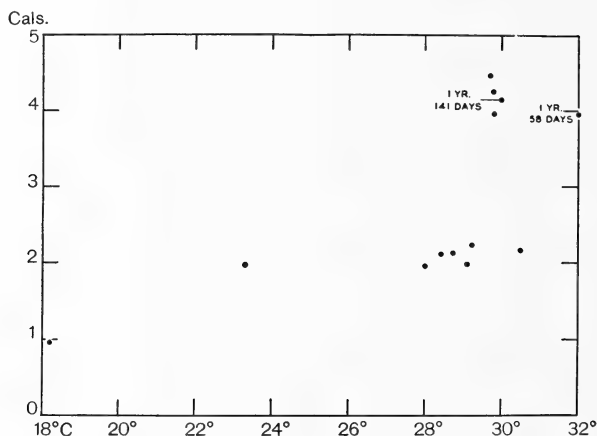


FIG. 44—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—Boa D.

#### STANDARD METABOLISM OF BOAS E AND F

Boas E and F were of nearly the same body weight, 4.86 and 5.73 kg., respectively. They were studied for a short time only. Boa E, it was believed, had been without food for more than two months. In fact, it had not eaten since it had arrived at the Park. It was, however, by no means emaciated. In the series of experiments with this boa (table 35) the range in temperature was small, from 20.0° to 24.1° C. All the periods were about 24 hours long. The differences in temperature are not large enough for one to expect to find any material changes in metabolism due to the temperature, although the metabolism in the series of October 18 to 23 is materially higher than that during October 12 to 15. Boa E was not used for any further experiments after October 23. No chart was prepared for this snake, but the values for its standard heat production will be used in subsequent comparisons. The heat production of this snake at the average temperature of 20.3° C. was 1.05 calories per kilogram of body weight per 24 hours. At 23.4°, the average of the second series of experiments was 1.35 calories.

With boa F only one experiment was made, on May 1, 1917. The results of this experiment are recorded along with the data for boa E, in table 35. The experiment began 14 days after the last food and con-

tinued 18 hours. The chief value of this particular test is its use for comparison with experiments made during digestion with this animal, which are to be considered later (p. 271). The experiment has one defect, in that the snake had been on the laboratory floor for several hours before the experiment began. Undoubtedly the floor temperature was several degrees below that at which the respiration experiment was made. The heat production determined during this 18-hour experiment averaged 1.15 calories per kilogram of body weight at an average temperature of 24.4°.

TABLE 35—*Standard metabolism of boas E and F*

Snake and date	Body weight	Days fasting	Period		CO <sub>2</sub> per kg. per 24 hours*	Heat produced per 24 hours		Environmental temperature
			No.	Length		Per kg.*	Per sq.m.*	
1916 Boa E:	<i>kg.</i>			<i>hrs.</i>	<i>gm.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
Oct. 12-13	4.86	60	1	20	0.315			20.0
Oct. 14-15	(4.86)	62	1	23	.314			20.6
Average						1.05	14.2	20.3
Oct. 18-19	4.83	66	1	24	.440			24.1
Oct. 19-20	(4.78)	67	2	23	.444			22.9
Oct. 20-21	(4.74)	68	3	24	.348			23.7
Oct. 21-22	(4.69)	69	4	24	.387			22.7
Oct. 22-23	(4.64)	70	5	24	.399			23.4
Average						1.35	18.3	23.4
1917 Boa F: May 1	5.73	14	1	18	.343	1.15	16.5	24.4

\* All the values in this column represent standard metabolism.

## STANDARD METABOLISM OF BOA G

Boa G, weighing 9.37 kg., was received at the Park on March 8, 1917, and it was assumed not to have fed for three weeks prior to its arrival. The first fasting experiment (see table 36) was made with it on March 19, but since the temperature of the environment to be studied was about 24° and the temperature of the reptile house and the den was nearer 28° C., high values appear in the first two periods of this experiment and standard values are not obtained until the third and fourth periods. Kymograph records showed that the boa was active during periods 5 and 8, which alone accounts for the high metabolism noted. On March 22 the effect of a higher temperature was studied. Boa G was active in the first period, which accounts for the high metabolism, and consequently the second, third and fourth periods only have been used for the standard values. On March 23, at a somewhat lower temperature, three of the four periods agree well. The fourth is high, with no explanation available. On March 24 the observations were continued at a slightly higher environmental temperature. Boa G was not used again until nearly a year later,

when it had lost considerable weight. Although it is reasonably certain that the boa used in May and June 1918 was the same as that studied in March 1917, it is difficult in a collection such as exists in a large park to

TABLE 36—*Metabolism of boa G—Fasting*

Date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1917			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Mar. 19 <sup>1</sup>	32 days	1	2	1.032	23.8
Mar. 19	9.37 kg.	2	8	.942	23.7
Mar. 19-20		3	6	* .631	24.2
Mar. 20		4	6	* .665	23.7
Mar. 20		5	7	.770	24.3
Mar. 20-21		6	7	* .581	23.6
Mar. 21		7	8	* .615	24.8
Mar. 21		8	6	.946	26.3
Mar. 22	35 days	1	3	1.069	29.4
Mar. 22	9.34 kg.	2	2	* .868	31.2
Mar. 22		3	3	* .807	33.0
Mar. 22		4	4	* .986	32.1
Mar. 23	36 days	1	3	*1.087	30.3
Mar. 23	9.31 kg.	2	3	*1.104	30.7
Mar. 23		3	3	*1.092	31.2
Mar. 23		4	3	*1.280	30.4
Mar. 24	37 days	1	4	*1.175	31.6
Mar. 24	9.28 kg.	2	3	*1.233	32.7
1918					
May 14 <sup>2</sup>	22 days	1	5	* .524	27.3
May 14-15	8.33 kg.	2	9	* .586	27.8
May 15		3	10	* .589	28.2
May 15		4	10	* .594	28.5
May 15-16		5	10	* .595	28.9
June 8 <sup>3</sup>	22 days	1	5	* .730	29.3
June 8	8.32 kg.	2	4	* .662	29.1
June 8		3	5	* .573	29.0
June 8		4	7	* .618	29.1
June 8-9		5	9	* .570	29.1

\* Only starred values represent standard metabolism.

<sup>1</sup> Boa was taken from reptile house at temperature of about 28° C. and put into cooler chamber at 12 noon, Mar. 19. First period began at 1<sup>h</sup>10<sup>m</sup> p.m.

<sup>2</sup> Boa was put into chamber at about 3 p.m., May 13. First period began at 1 p.m., May 14.

<sup>3</sup> Boa was put into chamber at 4 p.m., June 7. First period began at 1<sup>h</sup>10<sup>m</sup> a.m., June 8.

be sure of the identity of each animal, and a slight element of doubt always enters. It is difficult to tag or otherwise identify these animals, and yet the various keepers in general know them with surprising accuracy. Five well-agreeing periods at about 28° were obtained between May 14 and 16, 1918. There then followed a digestion experiment (not reported here)

and the next fasting experiment was made on June 8-9, with five satisfactory periods. The temperature in the rectum immediately after this experiment was 29.42°, that of the respiration chamber 29.13°, and that of the room 20.0°.

The average standard heat production of boa G per kilogram of body weight per 24 hours is recorded in table 37, the data being arranged in the order of increasing environmental temperatures. The entire temperature range with boa G was small, from 24° to 32° C. on the average. From a rough inspection of this table it can be seen that the highest metabolism is not found at the highest environmental temperature, nor the lowest metabolism at the lowest temperature. It is clear that boa G in 1918 was at a lower metabolic level than in 1917.

TABLE 37—Standard heat production of boa G

Date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq.m.	
1917-1918		<i>cals.</i>	<i>cals.</i>	°C.
Mar. 19-21	32	2.08	34.8	24.1
May 14-16	22	1.92	31.4	28.1
June 8-9	22	2.10	34.3	29.1
Mar. 23	36	3.80	64.3	30.7
Mar. 22	35	2.96	50.3	32.1
Mar. 24	37	4.02	67.8	32.2

<sup>1</sup> Derived from starved data in table 36.

#### STANDARD METABOLISM OF BOA H

Boa H arrived at the Park on March 8, 1917. It was fed about March 13. In the first experiment (table 38) the average environmental temperature was 19.6° C. The irregularity in the metabolism of this animal might be explained by pregnancy. The average carbon-dioxide value for the first two periods is not far from the values in the other periods, and probably represents the average metabolism at this temperature. For this reason the five periods have been averaged in computing the standard heat production per kilogram of body weight per 24 hours. About April 16 boa H gave birth to a litter of eighteen. The animal had fed well since this time, but the experiment on June 11-12 was made 7 days after food. The snake was in good condition, for the body weight was actually at a somewhat higher level than in March, in spite of the birth of the young. The rise in the temperature of the environment in the experiment of June 11-12 accounts for the increase in the carbon-dioxide production per kilogram of body weight. The last two periods are considered to represent the standard metabolism at an average temperature of 33.4° C. About midnight, June 12, a rabbit was offered to boa H, but was refused. The rectal temperature just before noon on June 13, after this attempted feeding, was 32.8° and the chamber temperature was 32.95° C.

Boa H was not studied again until nearly a year later, May 31, 1918, when it had undergone a considerable loss in body weight, 1.5 kg., although it was stated to have fed only 7 days before. The carbon-dioxide value of 0.691 gram in the third period is alone considered standard, as the temperature was continually rising. Between June 3 and June 7 considerable changes in the temperature were designedly made, in order to study the reaction

TABLE 38—*Metabolism of boa H—Fasting*

Date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1917			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Mar. 28 <sup>1</sup>	15 days	1	3	*0.411	19.3
Mar. 28-29	7.40 kg.	2	14½	*.129	19.4
Mar. 29		3	16	*.210	19.6
Mar. 29-30		4	23	*.156	19.9
Mar. 30-31	7.36 kg.	5	18	*.200	20.0
June 11-12	7 days	1	8	.946	28.5
June 12	7.99 kg.	2	6	1.033	31.7
June 12		3	5	*1.168	33.2
June 12		4	5	*1.196	33.7
1918					
May 31 <sup>2</sup>	7 days	1	9	.560	28.4
May 31-June 1	46.49 kg.	2	9	.523	29.3
June 1		3	10	*.691	30.5
June 3 <sup>5</sup>	10 days	1	5	*.782	31.6
June 3	46.49 kg.	2	5	*1.003	32.4
June 3-4		3	5	*1.124	32.6
June 4		4	9	*.954	32.0
June 4		5	7	*.814	31.2
June 4		6	6	*.876	30.4
June 4-5		7	11	.733	29.4
June 5		8	10	.760	27.9
June 5-6		9	13	.540	26.2
June 6		10	12	.514	24.5
June 6-7		11	13	.406	23.0

\* Only starred values represent standard metabolism.

<sup>1</sup> Boa was put into chamber Mar. 27 to remain overnight.

<sup>2</sup> There is no explanation for variation in carbon-dioxide, production Mar. 28-31. But boa pregnant. Eighteen born April 16.

<sup>3</sup> Boa may have been in chamber during night of May 30-31, but environmental temperature preceding experiment is not known.

<sup>4</sup> Weight obtained on May 30 and also on June 7, 1918.

<sup>5</sup> Boa apparently remained in chamber from June 1 to June 3. Temperature of environment June 3-7 was purposely altered to study effect of changes of environment.

of the metabolism to temperature. It was not considered that standard values were obtained after the first six periods, with such shifts in the temperature. The results do show, however, the characteristic decrease in metabolism with the accompanying fall in temperature, although it is by no means certain that the snake had really attained a uniform state. The observations with boa H on June 3 to 7 were of primary interest as

being preliminary to a digestive experiment made one month later. Boa H was about to shed at the close of the experiment on June 7. It is not known when the skin was shed. The rectal temperature at 11 a.m., June 7 (period 11 ended at 10<sup>h</sup>40<sup>m</sup> a.m.), was 22.73°; the chamber temperature was 22.31°, and the room temperature, 22.5° C.

With boa H the lowest environmental temperature was 20° and the highest 33° C. The calculations of the standard heat production are recorded in table 39. It is seen here that the metabolism is correspondingly low at the low temperature and higher at the higher temperatures. Only the starred values in table 38 are used in subsequent comparisons with other boas and other snakes, as representing a constant metabolic state.

TABLE 39—*Standard heat production of boas H and I*

Snake and date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq.m.	
1917-1918		<i>cals.</i>	<i>cals.</i>	°C.
Boa H:				
May 28-31	15	0.74	11.6	19.6
June 1	8	2.30	33.9	30.5
June 3-4	10	3.09	45.6	31.7
June 11-12	7	3.94	63.0	33.4
Boa I:				
Apr. 20-21	38	0.73	10.7	19.7
Apr. 23-24	41	.79	11.6	20.5
May 23-25	29	3.33	48.9	31.7
June 4-5	9	6.65	96.7	36.0

<sup>1</sup> Derived from starred data in tables 38 and 40.

#### STANDARD METABOLISM OF BOA I

The results for boa I are recorded in tables 39 and 40. Boa I arrived at the Park at the same time as boa H, that is, March 8, 1917. It was fed during March, and the last feeding day is assumed to have been March 13. Hence the first experiment with boa I on April 20-21 was made 38 days after food, when the snake weighed 6.15 kg. Both periods of this experiment were secured at a low temperature, under standard conditions. Two days later a slightly higher temperature was used in the study. There then followed a digestion period not reported here, and a fasting experiment was again made on May 23, when the animal had been 29 days without food. The first period of this experiment is left out of consideration, owing to the fact that the temperature was rising. Activity was recorded during period 5 and again during periods 7 and 8, accounting in part at least and probably in whole for the higher metabolism during these periods. An attempt was made to carry out an experiment at a very high environmental temperature, beginning June 4, and the snake had undoubtedly not attained a uniform temperature during the first and probably the second periods, as the temperature of the apparatus was



actually rising somewhat. Six periods at about 36°, one of the highest temperatures at which boas were studied, were finally obtained and for the most part they agree well.

At the close of the experiment on June 5, boa I was offered a rabbit and killed it, but did not swallow it. The rectal temperature was 36.63° C.

TABLE 40—*Metabolism of boa I—Fasting*

Date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1917			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Apr. 20–21 <sup>1</sup>	38 days	1	23	*0.259	19.7
Apr. 21	6.15 kg.	2	9	*.205	19.3
Apr. 23–24 <sup>2</sup>	41 days	1	18	*.285	20.5
Apr. 24	6.15 kg.	2	13	*.262	20.5
May 23 <sup>3</sup>	29 days	1	3	.526	29.1
May 23	6.02 kg.	2	8	*.990	32.1
May 23–24		3	10	*.828	32.3
May 24		4	8	*1.176	32.2
May 24–25		5	8	1.290	30.8
May 25		6	9	*.997	30.2
May 25		7	7	1.211	31.1
May 25–26		8	10	1.143	33.1
June 4 <sup>4</sup>	9 days	1	2	1.824	34.8
June 4	6.25 kg.	2	4	2.294	36.0
June 4–5		3	4	*2.246	36.4
June 5		4	6	*1.997	36.2
June 5		5	3	*2.068	35.8
June 5		6	4	*1.864	36.1
June 5		7	4	*1.993	35.9
June 5		8	3	*1.797	35.4

\* Only starred values represent standard metabolism.

<sup>1</sup> Boa was probably in box at laboratory during night of Apr. 19–20.

<sup>2</sup> Boa had remained in chamber since Apr. 21.

<sup>3</sup> Boa was put into chamber at midnight, May 22.

<sup>4</sup> Boa was probably put into chamber on June 4, and when experiment began was not at high temperature maintained during most of experiment.

some time the following morning after boa I had remained in the respiration chamber all night. The chamber temperature was 36.67° and the room temperature about 21° C.

With boa I, as seen in table 39, the lowest temperature was accompanied by the lowest metabolism and the highest temperature by the highest metabolism.

#### STANDARD METABOLISM OF BOA J

Boa J was used for a large number of experiments, many of them during digestion, between August 11, 1919, and February 12, 1920. During this time the body weight fell from 4.59 to 4.01 kg. on the last day of the experiments, with various fluctuations, varying in accordance with the feeding.

On the date of the first experiment, August 11, 1919, it was not known exactly how long boa J had been fasting. It was probably two months or more, and it has been assumed that the last feeding date was June 15. Boa J remained in the respiration chamber from August 11 through August 14, and twelve periods, of which the last ten give suitable standard values, were obtained at an average temperature of 28.7° C. (table 41). The rectal temperature of this snake, ten minutes after the close of the experiment on August 14, was 26.88° C. The room temperature then was 19.7°, and the chamber temperature 28.56° C. Thus the rectal temperature was

TABLE 41—*Metabolism of boa J—Fasting*<sup>1</sup>

Date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1919			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Aug. 11 <sup>1</sup>	56 days	1	2¾	0.989	26.8
Aug. 11	4.59 kg.	2	4¼	.703	27.5
Aug. 11-12		3	6¾	*.728	28.6
Aug. 12		4	7¼	*.592	28.7
Aug. 12	4.57 kg.	5	6¼	*.681	28.6
Aug. 12-13		6	6½	*.776	28.8
Aug. 13		7	8	*.524	28.7
Aug. 13		8	5	*.764	28.6
Aug. 13	4.55 kg.	9	6	*.833	28.9
Aug. 13-14		10	7	*.626	28.6
Aug. 14		11	8	*.675	28.5
Aug. 14	4.55 kg.	12	7	*.661	28.7
Aug. 15 <sup>2</sup>	60 days	1	3	.583	28.1
Aug. 15	4.54 kg.	2	6	.770	28.2
Aug. 15-16		3	7	*.838	28.7
Aug. 16		4	8	*.878	29.0
Aug. 16		5	6	*.775	28.8
Aug. 16		6	6	*.824	28.7
Aug. 16-17		7	7	*.807	28.8
Aug. 17		8	7	*.807	28.8
Aug. 22 <sup>3</sup>	67 days	1	6	*.843	27.6
Aug. 22	4.54 kg.	2	6	*1.049	28.6
Aug. 22-23		3	6	*1.043	28.7
Aug. 23		4	8	*.868	28.6
Aug. 23		5	6	*1.182	28.6
Aug. 23-24		6	7	*.797	28.7
Aug. 24		7	7	*1.044	28.6
Aug. 24		8	6	*1.144	28.3
Oct. 24 <sup>4</sup>	13 days	1	3	.714	27.5
Oct. 24-25	3.92 kg.	2	5	*.823	29.1
Oct. 25		3	5	*.827	29.7
Oct. 25		4	5	*.851	30.2
Oct. 25		5	5	*.840	29.5
Nov. 5 <sup>5</sup>	10 days	1	4	.753	27.1
Nov. 5	3.98 kg.	2	4	*.778	28.4
Nov. 5-6		3	6	*.783	28.9
Nov. 6		4	6	*.587	29.2
Nov. 6		5	6	*.702	29.4

<sup>1</sup>This table is continued on p. 176.

TABLE 41—*Metabolism of boa J—Fasting (Continued)*

Date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1919			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Dec. 1 <sup>6</sup>	16 days	1	4	.486	20.6
Dec. 1-2	4.09 kg.	2	13	* .321	21.1
Dec. 2-3		3	17	* .319	20.8
Dec. 3		4	17	* .232	20.7
Dec. 3-4		5	19	* .210	20.6
Dec. 4-5		6	25	* .251	20.6
Dec. 27 <sup>7</sup>	22 days	1	3	1.731	31.7
Dec. 27	3.64 kg.	2	5	1.391	31.5
Dec. 27		3	6	1.475	31.5
Dec. 27		4	8	*1.159	31.2
Dec. 27-28		5	10	*1.183	30.7
Dec. 28		6	7	*1.207	30.6
Dec. 28-29		7	8	* .999	30.4
Dec. 29		8	10	*1.261	30.7
Dec. 29		9	7	* .984	31.0

\* Only starred values represent standard metabolism.

<sup>1</sup> Boa was brought from reptile house and put into chamber at 2<sup>h</sup>15<sup>m</sup> p.m., Aug. 11. First period began 3 p.m.

<sup>2</sup> Boa was put back into chamber after rectal temperature was taken on August 14.

<sup>3</sup> Boa probably had not undergone any great change in temperature since last experiment.

<sup>4</sup> Boa was brought to laboratory and put into chamber at 3 p.m., Oct. 24. Chamber was closed at 5 p.m. First period began at 5<sup>h</sup>40<sup>m</sup> p.m. Temperature was fairly regular except that it rose 3° in period 1.

<sup>5</sup> Boa was probably put into chamber on Nov. 5.

<sup>6</sup> Boa had been in chamber since Nov. 27; was taken out to be weighed on Dec. 1. Chamber was closed at 2 p.m., Dec. 1. First period began 3 p.m., Dec. 1.

<sup>7</sup> Boa was returned to reptile house on Dec. 23; was brought to laboratory and put into chamber again at 1 p.m., Dec. 26. First period began at 1<sup>h</sup>30<sup>m</sup> a.m., Dec. 27.

almost 2° below the chamber temperature, and it is likely that the seeming discrepancy between the values found at this temperature on August 11 to 14 and those in the next series, August 15 to 17, may be accounted for by the fact that although the environmental temperature was the same, for some reason thus far unexplained the rectal temperature in the first series was much lower (2°) than the environment. In the second series, on the other hand, it was only half a degree below the environment, the rectal temperature being 28.32° on August 17, the chamber temperature 28.80°, and the room temperature 21.5° C. This is a striking illustration of the fact that frequently the environmental temperature does not represent the true body temperature of the snake, and that therefore all our comparisons of metabolism with temperature may be somewhat in error, because we are recording an environmental temperature and not a body temperature. But it was considered impracticable to disturb the snake at the end of each period during the experiment to determine the rectal temperature.

On August 22 still another series of three days was made at approximately the same temperature, 28° C. In all probability the boa had been at this

environmental temperature since August 17. The body weight was the same as before. In this experiment there were eight periods, of which the average value can properly be used. The metabolism was higher in this experiment than that in the previous series, August 15 to 17, which in turn was obviously somewhat higher than that in the series on August 11 to 14. Unfortunately rectal temperatures were not obtained in the experiment of August 22 to 24, but it is clear that although there was a constant environmental temperature averaging  $28.7^{\circ}$ , there was a great increase in metabolism between the first and the third series. It was found at the end of the experiment on August 24 that the boa was about to shed. It was therefore returned to the reptile house. It is not known when the skin was actually shed.

Two months later boa J was again used for a fasting experiment, but only 13 days since the last feeding. Owing to the irregularity in the temperature of the environment, the first period is not usable, but the four subsequent periods at an average temperature of  $29.6^{\circ}$  agree well. The next series, on November 5-6, was complicated by the fact that the temperature slowly rose. Nevertheless, the last four periods have been considered to represent standard conditions. On December 1, when boa J had been in the respiration chamber since November 27, it was taken out and weighed and put back. Here there is clear evidence of the result of the handling, inasmuch as the first period gives a high carbon-dioxide measurement. The five subsequent periods agree well on the whole and can be considered as representative of the standard metabolism at an average temperature of  $20.7^{\circ}$  C.

About three weeks later, December 27, another series of observations was made with boa J, but meanwhile it had been returned to the reptile house on December 23 and brought back to the laboratory and put into the chamber at 1 p.m., December 26. The first experimental period began at 1<sup>h</sup>30<sup>m</sup> a.m., December 27. The results for the first three periods are unusually high and have not been starred, although the first period began 12 hours after boa J had been placed in the chamber, and one would have expected that any agitation or disturbance due to handling would have passed off. At this high temperature there was an unusually slow adjustment to the new conditions. Again it is unfortunate that the rectal temperature was not taken. The average of the last six measurements, which are taken as standard, gives a high metabolism at the highest temperature thus far measured with this snake. The increase over the metabolism obtaining on August 11 to 14 at  $28.7^{\circ}$  or that on October 24 to 25 at  $29.6^{\circ}$  is great for an increase in temperature of only 2 degrees. This comparison shows the intense lability of the metabolism of these snakes. On the other hand, the body weight had decreased to 3.64 kg., indicating a loss of 21 per cent from the initial weight in August. One defect in these observations is the lack of adequate data for the comparison between environmental temperature and rectal temperature. Without doubt, referring the metabolism to the environmental temperature introduces an error, in that the rectal temperature is always a little and may at times be considerably below the environment. In the particular case of boa J whose

metabolism in the last fasting experiment was in some periods almost double that on August 11 to 14 (although the environmental temperature was only 2 degrees higher on the average), we are reminded of the fact that the rectal temperature in the first experiment was really about 2 degrees below the environmental temperature. In subsequent experiments with snakes, records of the environmental temperature should be only a part of the story, and one should really determine the rectal temperature at the end of the experiment in all cases.

The standard heat production of boa J, calculated per kilogram of body weight and per square meter of body surface per 24 hours, is given in table 42. These fasting values for boa J serve a dual purpose, not only as a

TABLE 42—*Standard heat production of boa J*

Date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq. m.	
1919		<i>cal.</i>	<i>cal.</i>	°C.
Dec. 1-5	16	0.89	11.4	20.7
Aug. 22-24	67	3.32	44.3	28.5
Aug. 11-14	56	2.29	29.9	28.7
Aug. 15-17	60	2.74	36.6	28.8
Nov. 5-6	10	2.38	30.6	29.0
Oct. 24-25	13	2.79	35.3	29.6
Dec. 27-29	22	3.77	47.3	30.8

<sup>1</sup> Derived from starred data in table 41.

study of the standard metabolism but as a baseline for comparison with the metabolism during numerous digestion experiments, for more digestion experiments were made with this boa than with any of the others. Since the experiments made at or near 29° show such a great range in the metabolism, it is particularly fortunate that standard values were obtained with this snake prior to each digestion experiment.

#### STANDARD METABOLISM OF BOA K

Our draft upon the New York Zoological Park animals became so heavy that a boa (K) was purchased from a circus by the Nutrition Laboratory on July 1, 1919. The first experiment was made with it on July 28, when it had been without food for presumably 10 days. It had eaten five rats shortly after July 15, and disgorged them some days before July 28. This tendency to disgorge food was noted on a subsequent occasion with this animal. But three fasting experiments were made with boa K (see tables 43 and 44). The initial body weight was 3.89 kg. On July 28, boa K was placed in the respiration chamber and the first period was started too soon after closing the chamber for the animal to reach a constant temperature. Hence the carbon-dioxide measurement in this period is high. The four subsequent periods agree reasonably well, with the highest value in the fifth period. Possibly a slightly higher environmental temperature may

have accounted for this. It has been assumed, however, that it is justifiable to average the last four periods.

The snake remained in the chamber continually, and another experiment on July 30 began at a somewhat lower temperature. In this experiment the environmental temperature apparently had not reached constancy at the end of the first period and hence there was a lower carbon-dioxide produc-

TABLE 43—*Metabolism of boas K and L—Fasting*

Snake and date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1919			hrs.	gm.	°C.
Boa K:					
July 28 <sup>1</sup>	10 days	1	4	1.777	28.8
July 28-29	3.89 kg.	2	6	*.952	28.3
July 29		3	7	*1.106	28.1
July 29		4	5	*1.105	28.4
July 29		5	5	*1.319	28.7
July 30 <sup>2</sup>	12 days	1	6	.750	26.9
July 30-31	3.84 kg.	2	9	*.883	28.6
July 31		3	9	*1.107	29.0
July 31		4	6	*.983	29.2
Aug. 1 <sup>3</sup>	14 days	1	8	*1.061	28.1
Aug. 1-2	3.79 kg.	2	8	*1.055	28.1
Aug. 2		3	12	*1.148	28.3
Boa L:					
Aug. 26 <sup>4</sup>	71 days	1	7	*.728	28.1
Aug. 26-27	4.05 kg.	2	8	*.762	28.5
Aug. 27		3	9	*.718	28.9
Aug. 27		4	9	*.822	29.2
Aug. 27-28		5	9	*.711	28.8
Aug. 28		6	8	*.638	28.5
Aug. 28	4.04 kg.	7	9	*.617	28.3
Aug. 28-29		8	10	*.688	28.5
Aug. 29		9	11	*.647	28.9
Aug. 29-30		10	9	*.732	28.7
Aug. 30		11	9	*.662	28.6

\* Only starred values represent standard metabolism.

<sup>1</sup> Boa K was put into chamber at 1<sup>h</sup>40<sup>m</sup> p.m., July 28. First period began at 2<sup>h</sup>10<sup>m</sup> p.m.

<sup>2</sup> Boa K probably remained in chamber in interval between experiments.

<sup>3</sup> Boa K apparently continued in chamber after experiment of July 30-31.

<sup>4</sup> Boa L was taken from reptile house on Aug. 25 and put into chamber.

tion in the first period than in subsequent periods, in conformity with the temperature. The three following periods give values that are sufficiently close to be averaged, representing the standard metabolism at an average temperature of 28.9° C. On August 1 still another experiment was made with three well-agreeing periods, at an average temperature of 28.2° C. When boa K was taken from the chamber at 5 p.m., August 2, the rectal temperature was 28.27°, the chamber temperature 28.34°, and the room temperature 23° C. A digestion experiment was made with boa K at the

end of this series and will be considered later (p. 287). On the whole, the three series of observations at approximately 28° represent a fairly close agreement in the values for the standard metabolism.

#### STANDARD METABOLISM OF BOA L

Boa L (initial weight 4.05 kg.) was taken from the reptile house on August 25, 1919, and placed in the respiration chamber. It had shed its skin on August 24. An experiment of 11 continuous periods, from August 26 to 30, was made at a fairly constant temperature. It is not known exactly how long the boa had been without food, except that it was recorded on August 18 that this boa had not been offered food for two months or

TABLE 44—*Standard heat production of boas K, L, M, and N*

Snake and date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq. m.	
1919-1920		<i>cal.</i>	<i>cal.</i>	°C.
Boa K:				
Aug. 1-2	14	3.63	45.9	28.2
July 28-29	10	3.74	46.9	28.4
July 30-31	12	3.30	42.2	28.9
Boa L:				
Aug. 26-30	71	2.34	29.6	28.6
Boa M:				
Dec. 30-Jan. 2	24	1.64	20.8	21.0
Feb. 10-13	25	1.65	20.1	21.5
Dec. 13-16	8	2.57	32.5	29.7
Boa N:				
Feb. 19	?	5.17	89.9	34.9
Feb. 18	?	5.49	94.4	36.0

<sup>1</sup> Derived from starred data in tables 43 and 45.

more. The fasting has therefore been assumed to date from June 15, that is, the snake had been fasting presumably 71 days at the beginning of the experiment. The results of the observations with boa L are recorded in tables 43 and 44. The carbon-dioxide measurements were all sufficiently close to justify considering them as standard values. At the end of the experiment on August 30 the rectal temperature was 27.9°, the chamber temperature 28.5°, and the room temperature 21.0° C. In this instance the rectal temperature was 0.6° below the temperature of the respiration chamber. Unfortunately the rate of ventilation and the measurement of the water vapor given off by boa L were not held under the closest control, so that it is not known whether the air was drier than in other experiments or whether there was a greater loss of water and a greater cooling effect. No further experiments were made with boa L, since it would not take food and hence could not be studied during the digestive cycle.

## STANDARD METABOLISM OF BOA M

Boa M weighed at the start 3.9 kg. It was placed in the respiration chamber at 2 p.m., December 13, and the first period began 7 hours later. During this time the snake had apparently adjusted itself to the temperature of the environment, for in 8 periods with little change in the temperature of

TABLE 45—*Metabolism of boas M and N—Fasting*

Snake and date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1919-20			hrs.	gm.	°C.
Boa M:					
Dec. 13-14 <sup>1</sup>	8 days	1	3	*0.694	29.2
Dec. 14	3.92 kg.	2	6	*.884	29.2
Dec. 14		3	8	*.801	29.0
Dec. 14		4	9	*.701	28.8
Dec. 14-15		5	13	*.715	30.2
Dec. 15		6	9	*.781	31.0
Dec. 15-16		7	8	*.987	30.6
Dec. 16		8	10	*.599	29.5
Dec. 30 <sup>2</sup>	24 days	1	7	*.558	20.4
Dec. 30	34.06 kg.	2	12	*.557	21.3
Dec. 30-31		3	15	*.453	21.4
Dec. 31		4	10	*.600	21.4
Dec. 31-Jan. 1		5	14	*.407	21.0
Jan. 1-2		6	13	*.385	20.7
Jan. 2		7	15	*.477	20.9
Feb. 8 <sup>4</sup>	25 days	1	13	.722	21.3
Feb. 8-9	3.41 kg.	2	16	.795	20.3
Feb. 9		3	13	.717	20.0
Feb. 9-10		4	17	.645	20.8
Feb. 10-11		5	16	*.481	20.7
Feb. 11		6	14	*.490	21.1
Feb. 11-12		7	15	*.505	21.9
Feb. 12-13		8	14	*.596	22.1
Feb. 13		9	14	*.401	21.7
Boa N:					
Feb. 18 <sup>5</sup>	<sup>6</sup>	1	1	*1.584	35.8
Feb. 18	10.15 kg.	2	3	*1.655	36.0
Feb. 18		3	3	*1.702	36.2
Feb. 19 <sup>7</sup>	10.08 kg.	1	3	*1.667	34.8
Feb. 19		2	4	*1.429	34.9

\* Only starred values represent standard metabolism.

<sup>1</sup> Boa M was put into chamber at 2 p.m., Dec. 13. First period began at 9h20m p.m., Dec. 13.

<sup>2</sup> Boa M was put into chamber at 3 p.m., Dec. 29. First period began at 3 a.m., Dec. 30.

<sup>3</sup> A weight of 3.86 kg. was obtained Jan. 4, 1920. Feces had been passed since last weight of 4.06 kg. on Dec. 29.

<sup>4</sup> Boa M had been returned to reptile house on Feb. 3 and was brought to laboratory again on Feb. 7. There was a long preliminary period of more than 6 hrs.

<sup>5</sup> In calorimeter at about 34° C. since afternoon of Feb. 17.

<sup>6</sup> Length of fast not known. Brought from New York to Boston Feb. 16, but no record when last fed.

<sup>7</sup> Boa N in chamber all night.



the environment the metabolism was sufficiently constant to be considered standard, although there were some rather considerable fluctuations, particularly in the first, seventh and eighth periods (see table 45). It is perhaps well at this point to call attention to the fact that all the measurements made with these animals represent differences in weights based upon a single set of readings. The weight of the absorbers was determined at the beginning and at the end of each period, but there were no duplicate readings. There was only a single, uncontrolled measurement by one observer, since many of the experimental periods began and terminated during the night. Every precaution was taken to read the weights correctly and to have the observer control his own weighings and readings, but the aberrant figures that sometimes occur may always be explained by some unsuspected error in weighing, for which, unfortunately, no absolute control was available.

After the experiment of December 13 to 16, boa M was taken out of the chamber for a few days. It was placed again in the respiration chamber at a lower temperature, at 3 p.m., December 29, and the first period began at 3 a.m., December 30, at an average temperature of 21° C. A series of 7 well-agreeing periods gives the standard metabolism at this temperature level. Boa M ate 7 rats on December 23 and 25, but they were disgorged on December 28, apparently not digested. Consequently it is argued that boa M had been 24 days without food on December 30. If one assumes that the rats were in part digested, then the length of time since the last food decreases to 6 days.

Boa M was brought to the laboratory again on February 7. It had shed its skin sometime after February 5. The boa was placed in the respiration chamber at a temperature of about 21°, but the decreasing carbon-dioxide production indicates that considerable time was required for the snake to adjust itself to its new environment. The last 5 periods, however, are representative of the standard metabolism at 21.5° C. The standard heat production (table 44, p. 180) in this experiment is not materially different from that found in the earlier experiment of December 30 to January 2, and confirms the belief that the rats eaten and disgorged December 28 had not been absorbed.

#### STANDARD METABOLISM OF BOA N

The experiments with boa N were made at the Nutrition Laboratory in Boston, inside of the emission calorimeter. The snake had been brought from New York and had been placed in the calorimeter at about 34° C. on the afternoon of February 17, 1920. The importance of making an experiment with these cold-blooded animals at a very high temperature was such that we felt justified in trying at least one with this boa. On February 18, therefore, such an experiment was made (tables 44 and 45) and fortunately three satisfactory periods were obtained at a temperature of approximately 36° C. No information is at hand as to how long boa N had fasted. At the end of the first experiment it was left in the chamber, and two other well-agreeing periods were obtained on February 19, at an average temperature of 34.9° C. Boa N was used for a number of other experiments, chiefly to study the influence of rapid variations in the temperature of the en-

vironment, the water output, and to compare the skin and the rectal temperature, most of which experiments have been treated in the section on the water output of serpents (p. 116). No digestion experiments were made with boa N.

## STANDARD METABOLISM OF GOPHER SNAKES

The American gopher snake is common, readily obtainable and easily handled. Since we desired to study a group of snakes, three gopher snakes

TABLE 46—*Metabolism of gopher snakes—Fasting*

Number of snakes and date	Days fasting and body weight	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
		No.	Length		
1917			hrs.	gm.	°C.
3 Snakes:					
Jan. 2 <sup>1</sup>	6 days	1	4	0.877	22.3
Jan. 2-3	5.76 kg.	2	10	*.732	22.1
Jan. 3		3	12	*.715	22.5
Jan. 3-4	5.74 kg.	4	12	*.691	22.3
Jan. 4		5	13	.842	22.8
Jan. 4-5	5.73 kg.	6	14	.826	22.4
Jan. 5	5.71 kg.	7	14	.988	22.6
Jan. 5-6 <sup>2</sup>		8	17	.758	23.2
Jan. 8-9	12 days	1	24	*.343	16.6
Jan. 9-10	5.71 kg.	2	26	*.390	17.1
Jan. 10-11		3	22	*.369	17.0
3 Snakes:					
Feb. 5	6 days	1	3	1.338	29.2
Feb. 5	6.11 kg.	2	3	1.199	30.0
Feb. 5-6		3	3	1.376	31.4
Feb. 6		4	6	2.034	30.2
Feb. 6		5	5	*1.829	30.3
Feb. 6		6	4	*1.775	29.5
Feb. 6		7	5	*1.754	31.2
Feb. 6-7		8	5	2.156	30.6
Feb. 7		9	6	2.828	29.0
Feb. 7		10	5	*1.736	29.9
1919					
1 Snake:					
Sept. 8	5 days	1	6	1.007	27.0
Sept. 8-9	2.86 kg.	2	8	*1.267	27.9
Sept. 9		3	10	*1.254	28.7
Sept. 9		4	9	*1.163	28.8

\* Only starred values represent standard metabolism.

<sup>1</sup> Snakes were put in chamber at 11<sup>h</sup>45<sup>m</sup> a.m., Jan. 2. First period began at 1<sup>h</sup>45<sup>m</sup> p.m.

<sup>2</sup> Chamber was opened after experiment, but snakes were left in chamber to cool.

were placed in the respiration chamber at 11<sup>h</sup>45<sup>m</sup> a.m. on January 2, at a temperature of 22° C. The first period began at 1<sup>h</sup>45<sup>m</sup> p.m. and, as shown in table 46, the carbon-dioxide production was affected by the previous handling. The gopher snakes were in general much more active than either the pythons or the boas, particularly the boas. This emphasizes again the disadvantage of studying the effect of environmental temperature with *small* cold-blooded animals and the special value of *large* snakes in such

studies. Thus, in the first series of observations with these snakes only the second, third and fourth periods can be considered as unaffected by previous handling and activity and can serve as standard values. At the end of the experiment on January 6 the chamber was opened, but the snakes were left inside to cool. One snake had started to shed at the close of this experiment and was expected to be through shedding in one or two days. The temperature was lowered rapidly after the measurements on January 6, and a second experiment began with these three gopher snakes on January 8, at a temperature of about 17° C. At this lower temperature no activity was recorded, and three well-agreeing periods were obtained. At the end of the experiment on January 11 it was found that two snakes had started to shed.

On February 5 three gopher snakes were again studied. One or even two of these may have been the same snakes studied in January. The

TABLE 47—*Standard heat production of gopher snakes*

Snakes and date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq.m.	
1917		<i>cal.</i>	<i>cal.</i>	°C.
3 Snakes:				
Jan. 8-11	12	1.22	12.2	16.9
Jan. 2-4	6	2.37	23.9	22.3
Feb. 5-6	6	5.92	60.4	30.2
1 Snake:				
Sept. 8-9	5	4.09	46.8	28.5

<sup>1</sup> Derived from starred data in table 46.

temperature was much higher, approximately 30°, and there was an extraordinary difference in the metabolism from period to period. Each period was not far from 4 hours long. The minimum carbon-dioxide production per kilogram of body weight per 24 hours was 1.199 grams and the maximum 2.828 grams. In the first three periods the metabolism was lower than in the succeeding periods. Unfortunately at this time the notes were very meager, for a series of experiments with the small Indian python during the digestive cycle was being carried out simultaneously, and these gopher snakes were considered as of secondary importance. The fourth period was characterized by considerable activity, as were likewise the eighth and ninth periods. From the protocols it would appear, however, as if the fifth, sixth, seventh, and tenth periods might well be used as representing the standard metabolism of these snakes at the average environmental temperature of 30.2° C.

In September 1919, one fairly large gopher snake was studied for four periods, at a temperature of approximately 28° C. The results for the last three periods are sufficiently uniform to be averaged. This particular gopher snake figured prominently in a number of digestion experiments, as

it was an excellent feeder. The snake had eaten three sparrows on the afternoon of September 3, and probably had not fed for four or five days since then, as it was the habit of these gopher snakes to eat only every four or five days. Probably the digestive cycle had passed, and it is reasonably certain that the snake was in the post-absorptive state. Comparison of the data obtained on this one snake with the measurements secured with the group of three snakes (fig. 63, p. 237) shows that the metabolism in the September experiment was not far from the probable average metabolism at 28° C. If anything, the metabolism was somewhat low rather than high, all of which points to the probable absence of stimulus due to digestive activity.

The standard heat production per 24 hours at the several temperatures, calculated from the averages of the starred carbon-dioxide values in table 46 and referred both to unit of body weight and to unit of body surface, is recorded in table 47. There are no data for gopher snakes to permit a study of the course of the metabolism of any one snake, as was done with the boas, and comparison of these gopher snakes will therefore be deferred until later (p. 237), when the results for each species of snakes as a whole will be considered.

#### STANDARD METABOLISM OF RATTLESNAKES

As the research progressed, it became increasingly important to note the metabolism of large snakes at the highest possible environmental temperature, when the body temperature would approximate that of a man or other warm-blooded animals. The great cost of the larger snakes in the Park made it undesirable to jeopardize possibly their lives by experiments at very high temperatures. Even the boas were studied at the high temperatures only with apprehension. It was finally decided to secure some rattlesnakes (*Crotalus atrox*), as they could be obtained readily at a not prohibitive price from the markets in Texas, and because they live normally under a high environmental temperature, from which fact it was argued that they might withstand the higher temperatures better than the other serpents. Rattlesnakes, being denizens of the desert, are accustomed to hot sand and hot sunlight, and are, *a priori*, better able to endure high temperatures than snakes, such as the boas, that live under trees in a shaded forest.

At the outset the problem of handling these dangerous rattlesnakes became acute. They are perhaps the most fatally poisonous of the American snakes, have a wicked temperament, and are ready to strike anything viciously. The handling of these snakes was therefore difficult. Indeed, the two men most skilful in handling snakes at the New York Zoological Park during the period of our research, Mr. Charles E. Snyder and Mr. John Toomey, were both subsequently struck by rattlesnakes. Mr. Snyder was fatally struck in a hunt for rattlesnakes to replenish the Park stock. Mr. Toomey was struck by a snake in the Park in one of the cages, and his life was saved only with the greatest difficulty. Our rattlesnakes were handled exclusively by Mr. Snyder and Mr. Edward L. Fox of the Nutrition Laboratory. To facilitate placing the snakes in the respiration chamber, particularly when two were studied simultaneously (as was the case in

many experiments), a wooden box without top or bottom was placed on top of the regular snake box in the respiration chamber. The walls of the snake compartment were thus elevated and the rattlesnakes could not easily escape when put into the chamber. When the snakes became quiet, a slide was inserted between the wooden box and the copper chamber, the wooden box was removed, and a wire-gauze cover fastened over the copper chamber. The difficulty of handling these poisonous reptiles restricted us considerably in the experimental program that we had hoped to carry out with them, but the most important feature was the metabolism at high temperatures, a reasonably clear picture of which was fortunately obtained.

Two large rattlesnakes, weighing together 10.45 kg., were placed in the respiration chamber, to study the effect of various temperatures. The first experiment was made in December 1915 (see table 48). The animals had arrived at the Park only two days before the observations began and were perhaps somewhat chilled on being brought from Texas. It was assumed that they had not been fed for at least three weeks on their arrival at the Park, but they may not have eaten since capture. The temperature of the environment in the first period on December 27 was  $36.8^{\circ}$  and the carbon-dioxide production per kilogram of body weight per 24 hours was 1.482 grams. A second period of five hours at a temperature 4 degrees lower gave a somewhat lower carbon-dioxide production. On December 28 and on three subsequent days the temperatures were held reasonably constant at from  $28.5^{\circ}$  to  $30^{\circ}$ . Four experiments, each of from 8 to 10 hours, gave fairly closely agreeing results. On taking the snakes out of the respiration chamber following the experiment on January 1, a number of ticks were found. The rattlesnakes were put back into the chamber again on January 5, but at a considerably lower temperature, nearer  $16^{\circ}$  or  $17^{\circ}$ , where they remained from January 5 to January 9. During this time four well-agreeing periods were secured, each of from 14 to 20 hours' duration. On January 14 the rattlesnakes were weighed again and placed in the chamber at a temperature of  $29.7^{\circ}$ , and an 11-hour period gave a standard value. On intermittent days from there on through February 18-19 the snakes were placed in the chamber and experiments ranging in length from 13 to 24 hours were made at various temperatures. In all the observations the snakes were fasting, and the results were sufficiently uncontaminated by activity to be considered as representing the standard metabolism.

Another series of measurements was made beginning December 5, 1916, with two much smaller rattlesnakes, which had been approximately 21 days without food. There were 15 consecutive periods, the first seven being at a practically constant temperature averaging  $21.8^{\circ}$ , and the last eight at a much higher temperature, averaging  $31.5^{\circ}$  C. Standard values were obtained at both levels, although in the transition period a characteristic change in the carbon-dioxide production was noted. On December 9 at the end of the experiment, the rattlesnakes were taken from the chamber and shaken thoroughly in the snake box, in order to agitate them. They had previously been at about  $32^{\circ}$ , but the environmental temperature during the experiment following the agitation unfortunately was lowered, so that when the snakes were under observation the normally appearing in-

TABLE 48—*Metabolism of rattlesnakes—Fasting*  
(Two snakes measured together in each experiment)

Date	Total body weight	Days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
			No.	Length		
1915	kg.			hrs.	gm.	°C.
Dec. 27	10.45	23	1	3	1.482	36.8
			2	5	*1.373	32.9
Dec. 28		24		9	*1.009	28.5
Dec. 29		25		10	*.962	30.1
Dec. 30		26		8	*1.030	29.6
Dec. 31		27		10	*1.038	28.2
1916						
Jan. 1		28		9	*1.143	29.7
Jan. 5-6	10.45	32		20	*.284	17.0
Jan. 6-7	(10.42)	33		14	*.212	16.1
Jan. 7-8	(10.39)	34		16	*.221	16.4
Jan. 8-9	(10.37)	35		15	*.241	17.1
Jan. 14	10.23	41		11	*.908	29.7
Jan. 15-16	10.15	42		14	*.663	22.5
Jan. 20-21	10.09	47		22	*.608	21.6
Jan. 28-29	10.04	55		24	*.200	15.0
Feb. 1-2	10.04	59		13	*.221	16.6
Feb. 5-6	10.01	63		18	*1.471	30.1
Feb. 7-8	9.92	65		16	*1.962	35.0
Feb. 11-12	9.84	69		18	*1.068	30.0
Feb. 12-13	9.84	70		19	*1.894	33.5
Feb. 16-17	9.81	74		23	*.568	21.6
Feb. 18-19	9.75	76		15	*1.244	27.6
Dec. 5 <sup>2</sup>	5.88	ca. 21	1	4	1.075	22.2
Dec. 5-6			2	7	.759	21.7
Dec. 6			3	6	*.687	21.7
Dec. 6			4	6	*.642	21.8
Dec. 6			5	8	*.667	22.0
Dec. 6-7			6	10	*.596	22.0
Dec. 7			7	9	*.607	21.6
Dec. 7			8	2	.577	30.5
Dec. 7-8			9	8	.865	32.2
Dec. 8			10	6	*1.472	32.2
Dec. 8			11	6	*1.449	30.6
Dec. 8			12	5	*1.420	31.2
Dec. 8-9			13	6	*1.437	31.1
Dec. 9	5.88		14	8	*1.409	31.7
Dec. 9			15	7	1.940	32.2
Dec. 9 <sup>3</sup>		ca. 25	1	3	1.163	27.9
Dec. 9-10			2	3	*1.038	27.7
Dec. 10			3	3	*1.060	27.3
Dec. 10			4	6	*.942	27.4
1917						
Jan. 12	5.94	<sup>4</sup>	1	3	*2.233	38.2
Jan. 12			2	4	*2.776	40.2
Jan. 12			3	3	4.040	40.5
Jan. 12			4	3	<sup>5</sup>	41.0

\* Only starred values represent standard metabolism.

<sup>1</sup> Temperature computed for first period is probably too high and snakes were probably not warmed to that point.<sup>2</sup> It is not known what the environmental temperature had been when snakes were put into chamber on Dec. 5.<sup>3</sup> Snakes taken from chamber and shaken well. Environmental temperature was lowered. Snakes active when put back into chamber, but soon became quiet.<sup>4</sup> One snake had been fasting at least 3 days and the other probably at least 7 days.<sup>5</sup> Snakes died, probably not at same time; one may have been alive at end of experiment.

crease in metabolism caused by the agitation was offset in large part by the decrease in temperature. The temperature remained sufficiently constant at about  $27.5^{\circ}$  to give three well-agreeing standard periods after the first period.

A month later another pair of rattlesnakes, not necessarily the same ones, were placed in the chamber in an attempt to secure a very high environmental temperature. One rattlesnake had been without food for at least three days, the other for at least seven days, probably much longer. The temperature of the environment was the highest thus far used with rattlesnakes, that is, from  $38^{\circ}$  to  $41^{\circ}$  C. At  $38.2^{\circ}$  and at  $40.2^{\circ}$  sufficiently satisfactory periods were obtained to secure standard metabolism values. At  $40.5^{\circ}$  there was activity, and during the last period the snakes died, possibly because of inefficient ventilation and excess carbon dioxide, but probably because of lack of suitable heat regulation and vaporization of water. In the respiration experiments at this time, altogether too little attention was paid to water-vapor conditions, the removal of the water vapor from the ventilating air current, and the degree of humidity in the air.

The rattlesnakes gave frequent indications of slight activity, much more so than the boas as a whole, so that in all probability, especially when two rattlesnakes were studied together, the metabolism was a little high. We do not feel justified, however, in attempting to make any correction. With the feeling that it was better to study one snake than two and in view of the large amount of carbon dioxide excreted by these snakes when the temperatures were around  $40^{\circ}$ , we carried out another series of measurements with individual rattlesnakes at high temperatures. The results are recorded in table 49. The first experiment with a single rattlesnake was on January 17, 1917. This snake, designated as rattlesnake A, weighed 2.95 kg. and with it very high environmental temperatures were attempted, even at the beginning. Rattlesnake A withstood three experiments, each of not less than six hours, at temperatures of  $37.3^{\circ}$  C. and over, but died shortly after the last experiment on January 25. As was to be expected, at these high temperatures rattlesnake A was frequently very active, and hence few periods can be selected as being free from activity and suitable for comparing the metabolism at different temperatures. Such periods are starred in the table. The relatively great height to which the metabolism of these cold-blooded snakes can rise when the environmental temperature is high is noted especially in the experiments of January 17 and January 25. In the former case the carbon-dioxide production per kilogram of body weight per 24 hours was 8.763 grams in the sixth period. This corresponds to nearly 30 calories per kilogram of body weight per 24 hours, or essentially the basal heat production per kilogram of an adult human. But in this period the rattlesnake was excessively active and a great deal of moisture was found in the chamber at the end of the experiment. Although there was some delay in taking the rectal temperature of the snake, it was recorded about 15 minutes after the experiment and was found to be  $38.6^{\circ}$  C. The room temperature was  $20.4^{\circ}$  C. Undoubtedly part of this fall was due to the environment, and yet we believe the rectal temperature was still definitely below the environmental temperature in the respiration chamber.

This large carbon-dioxide production, therefore, is a resultant of the high environmental temperature and the activity. Indeed, in this experiment of January 17 there was a continually increasing production of carbon dioxide,

TABLE 49—*Metabolism of rattlesnakes—Fasting*  
(Measured individually)

Snake, date, weight and days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environ- mental tempera- ture	Snake, date, weight and days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environ- mental tempera- ture
	No.	Length				No.	Length		
1917		hrs.	gm.	°C.	1917		hrs.	gm.	°C.
Rattlesnake A:	1	1	*2.197	37.3	Rattlesnake C:	1	5	*2.419	34.3
Jan. 17	2	1	3.742	38.4	June 13-14 <sup>5</sup>	2	4	*2.454	35.2
2.95 kg.	3	1	4.637	39.3	5.47 kg.	3	3	*2.715	35.2
<sup>1</sup>	4	1	5.939	40.2	44 days <sup>6</sup>	4	5	*2.357	34.7
	5	1	7.892	40.1	(5.42 kg.)	5	5	*2.326	35.2
	6	1	8.763	40.3	June 14-15	6	11	*2.552	36.4
					June 15	7	4	*2.530	36.9
Jan. 24 <sup>2</sup>	1	1	*4.000	41.5	(5.37 kg.)	8	3	*2.734	36.5
2.94 kg.	2	1	*3.510	42.4		9	4	*2.492	37.1
<sup>1</sup>	3	1	5.959	42.9	June 15-16	10	4	3.239	38.0
	4	1	5.877	43.4	June 16	11	5	3.468	38.7
	5	1	5.306	43.1		12	5	5.227	39.2
	6	1	4.082	42.9		13	4	5.266	39.5
	7	2	3.801	44.0					
Jan. 25 <sup>3</sup>	1	3	6.091	42.2	June 29 <sup>7</sup>	1	9	*4.388	36.0
2.90 kg.	2	2	*4.202	43.2	5.18 kg.				
<sup>1</sup>	3	3	5.318	42.3	60 days <sup>6</sup>				
Rattlesnake B:					Rattlesnake D:				
Jan. 30	1	2	4.133	42.9	July 1	1	4	2.640	36
2.41 kg.	2	2	4.880	44.2	3.54 kg.	2	3	*3.909	38.2
<sup>1</sup>	3	2	*3.784	44.2	62 days <sup>6</sup>	3	3	*4.384	38.0
					July 2	4	4	*4.458	38.6
						5	4	*4.732	39.8
Jan. 31 <sup>4</sup>	1	2	*3.795	43.0		6	5	*4.488	38.0
2.34 kg.	2	2	5.026	43.9	(3.51 kg.)	7	3	5.043	38.7
<sup>1</sup>	3	2	3.333	44.0		8	4	5.118	39.8
					July 2-3	9	5	5.248	38.0
					July 3	10	4	<sup>8</sup>	37.5

\* Only starred values represent standard metabolism.

<sup>1</sup> Length of fast of rattlesnakes A and B not known.

<sup>2</sup> Remained during night of Jan. 23-24 at temperature of about 36° C.

<sup>3</sup> Snake found dead on Jan. 26.

<sup>4</sup> Snake found dead at end of experiment.

<sup>5</sup> Snake was put into respiration chamber sometime in morning, June 13.

<sup>6</sup> Days fasting computed from May 1, when snake arrived at Park. There was no record of feeding since arrival.

<sup>7</sup> Snake apparently died soon after end of first period.

<sup>8</sup> Snake died during experiment, probably during period 10.

which was closely correlated with the increased activity. It seems inconceivable, however, that activity could account for a production of carbon dioxide in the sixth period more than four times that in the first period, and undoubtedly the lower metabolism at the beginning of the experiment is explained by the fact that in the first period the environmental temperature was at least 3 degrees lower than in the last.



On January 24 rattlesnake A had been at a high temperature of about  $36^{\circ}$  since the night before. The metabolism in the first two periods was uncontaminated by activity. The snake then became restless and remained so until the seventh period, when it was again quiet. Unfortunately, however, this period can not be starred as standard, for the environmental temperature rose a whole degree over that in the sixth period. On January 25 an experiment of three periods was made likewise at a high temperature, of which only one period can be considered as standard, owing to the complication of activity. Rattlesnake A was in good condition and lively at 11 p.m., January 25, five hours after the experiment ended, but it was found dead at 10 a.m., January 26. It had been in an open cage during the night of January 25-26 at about  $37^{\circ}$  in a thermostatically controlled chamber, partly covered with a blanket.

On January 30 another individual rattlesnake, B, was studied, weighing 2.41 kg. Again high temperatures prevailed, but only one period could be accepted as standard. Rattlesnake B was used on the next day at about the same temperature, and again one standard period was obtained, confirming exactly that of the day before. The snake died during the last period and in this period the carbon-dioxide production was much lower than that in the second period.

On June 13 another rattlesnake, C, was placed in the respiration chamber some time during the morning. The preliminary period began at 11<sup>h</sup>25<sup>m</sup> p.m. and lasted 30 minutes. The snake was nearly through shedding when put into the box, but the skin still hung loosely to its body. The skin, completely shed and weighing 85 grams, was found in the chamber at the end of the experiment. The temperature was materially lower than in the preceding experiments, averaging for the first part of this series about  $35^{\circ}$ , gradually going up to  $38^{\circ}$  or  $39^{\circ}$  C. In the first nine periods, rattlesnake C was sufficiently quiet and unaffected by previous disturbance for the results to be used as standard values and averaged. The other periods were contaminated by a continually rising temperature. The rectal temperature after the experiment was  $39.3^{\circ}$ . The temperature of the chamber was  $39.64^{\circ}$ , and that of the room  $21.4^{\circ}$  C. The snake showed great lassitude at the time the rectal temperature was taken.

On June 29 rattlesnake C, which had fallen from an initial weight of 5.47 kg. to 5.18 kg., was put into the chamber for three periods at  $36^{\circ}$ . On this date it had been about 60 days without food. The first period of 9 hours is considered standard. The second and third periods were 3 and 7 hours long, respectively, but less than 1 gram of carbon dioxide was collected in each period and the results are accordingly not reported. The snake died during the experiment, probably during the second or the third period, as there was some slight activity at the end of the first period.

On July 1 a fourth rattlesnake, D, weighing 3.54 kg., was placed in the respiration chamber at a temperature that was gradually increased from  $36^{\circ}$  to  $39^{\circ}$  C. From the second to the sixth period the snake was sufficiently free from activity for the results to be considered standard. The snake died during period 10.

Although these rattlesnakes could be exposed to a much higher temperature than the pythons and boas, these high temperatures were fatal,

particularly under the conditions prevailing during the measurements. It is possible that had an open-circuit apparatus been employed and had the ventilation been increased to keep the humidity very low, the outcome might have been different. In many instances when the respiration chamber was opened after the experiment, it was found that the snake was covered with a large amount of moisture. Under these conditions the tem-

TABLE 50—*Standard heat production of rattlesnakes*

Snakes and date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq. m.	
1915-1917		<i>cal.</i>	<i>cal.</i>	°C.
2 Snakes:				
Jan. 28-29	55	0.67	9.1	15.0
Jan. 6-7	33	.71	9.7	16.1
Jan. 7-8	34	.74	10.1	16.4
Feb. 1-2	59	.74	10.0	16.6
Jan. 5-6	32	.95	13.1	17.0
Jan. 8-9	35	.80	10.9	17.1
Jan. 20-21	47	2.03	27.7	21.6
Feb. 16-17	74	1.89	25.8	21.6
Dec. 6-7	22	2.13	25.0	21.8
Jan. 15-16	42	2.21	30.3	22.5
Dec. 9-10	25	3.38	39.7	27.5
Feb. 18-19	76	4.15	56.3	27.6
Dec. 28-31	24	3.37	46.4	29.1
Jan. 1	28	3.81	52.4	29.7
Jan. 14	41	3.03	41.9	29.7
Feb. 11-12	69	3.56	48.7	30.0
Feb. 5-6	63	4.90	66.3	30.1
Dec. 8-9	24	4.79	56.3	31.4
Dec. 27	23	4.58	63.0	32.9
Feb. 12-13	70	6.31	86.2	33.5
Feb. 7-8	65	6.54	87.7	35.0
Jan. 12	5	8.35	95.4	39.2
C, June 13-15	44	8.36	116.2	35.7
C, June 29	60	14.63	199.4	36.0
A, Jan. 17		7.32	83.1	37.3
D, July 1-2	62	14.65	178.8	38.6
A, Jan. 24		12.52	141.6	42.0
B, Jan. 31		12.65	134.6	43.0
A, Jan. 25		14.01	162.5	43.2
B, Jan. 30		12.61	138.1	44.2

<sup>1</sup> Derived from starred data in tables 48 and 49.

perature regulation of the animal must have been very poor. The few experiments with rattlesnakes do, however, enable the projection of the temperature scale for snakes to a point much farther than it was possible to do for either boas or pythons.

The average standard heat production of these rattlesnakes has been computed as usual from the standard carbon-dioxide production, and the results, both per unit of weight and per unit of surface area, are recorded in table 50. There are not enough data for any one rattlesnake to enable

a study of the individuality in metabolism of a given snake, and discussion of these rattlesnakes as a whole will be deferred until a later section (see pages 238 and 242), where the standard metabolism of snakes of the same and different species will be compared.

#### STANDARD METABOLISM OF A SMALL INDIAN PYTHON

The python, of which the small Indian python (*Python molurus*) that we studied was an admirable example, is in general an irritable, almost savage snake, in contrast to most boas. This particular small Indian python exhibited unusual agitation, anxiety and cleverness. The standard method of removing the snake from the den was to throw a blanket over its coiled body; then the keeper reached under the blanket, took hold of the snake's head and pulled the snake out. The small Indian python quickly learned to crawl out over the other side after the blanket was thrown on it, and frequently we were faced with the head of the snake on the opposite side of the blanket, looking toward us. Indeed, the savageness and disposition of this python to resist capture or handling led to our nicknaming it "Pepper."

With the small Indian python the length of period varied from a minimum of 2 hours to a maximum of 38½ hours, depending almost entirely upon the temperature of the environment. Thus, at 16° to 17° C., periods of from 20 to 28 hours were necessary, and at much higher temperatures 3 to 6 hours were usually sufficient. The results of the carbon-dioxide measurements on the small Indian python are recorded in table 51. The starred values are those made during periods fulfilling the conditions for "standard metabolism" measurements, as outlined on page 155. Hence they are suitable for a study of the influence of environmental temperature upon metabolism, uncontaminated by previous agitation or temperature readjustment. The experiments are reported in the table chronologically, from which it can be seen that the research on the standard metabolism of the small Indian python continued from November 6, 1915, to February 27, 1917, approximately 16 months. During this time there were fairly long periods of abstinence from food, but food was taken on several occasions, as is shown by the differences in the table column for days fasting.

#### BODY-WEIGHT CHANGES

There were marked changes in the weight of this python. The highest weight, 7.43 kg., was noted on November 6, 1915, the date of the first experiment, and again on April 8-9, 1916. Thereafter the body weight decreased. The final body weight of 5.95 kg. on February 26, 1917, is but a few grams higher than the minimum weight of 5.82 kg. on January 31, 1917. These changes in body weight are closely associated with the taking of food and long fasting. The change in weight, from a maximum of 7.43 kg. to a minimum of 5.82 kg., is such that it is possible to study the influence of size upon the metabolism of this fasting snake. The longest period of fasting in which the metabolism was measured was when the python had been 149 days without food, on February 24-25, 1916. This, however, as will be seen in later studies, is not an excessive length of time

TABLE 51—*Metabolism of small Indian python—Fasting*

Date	Body weight	Days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
			No.	Length		
1915	<i>kg.</i>			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Nov. 6	7.43	39	1	5	*1.815	34.0
Nov. 7	7.43	40	1	6	*2.013	35.0
Nov. 8	7.43	41	1	6	*1.973	35.5
Nov. 9	7.43	42	1	5	*1.698	35.0
Nov. 11	7.43	44	1	6	*1.413	35.0
Nov. 12	7.43	45	1	6	*1.288	36.0
Nov. 13	7.43	46	1	6	*1.428	35.5
1916						
Jan. 25-26	7.00	119	1	13	*.349	20.5
Jan. 26-27	7.00	120	1	17	*.300	20.7
Jan. 31-Feb. 1	6.97	125	1	28	*.171	16.5
Feb. 2-3	6.95	127	1	16	*.615	29.0
Feb. 4-5	6.95	129	1	18	*.647	29.5
Feb. 8-9	6.89	133	1	18	*.936	34.0
Feb. 14-15	6.83	139	1	17	*1.057	35.0
Feb. 17-18	6.80	142	1	19	*.293	20.7
Feb. 21-23	6.75	146	1	38	*.297	20.1
Feb. 24-25	6.69	149	1	23	*.197	15.4
Apr. 8-9	7.43	30	1	21	*.568	21.9
Apr. 18-19	7.37	40	1	21	*.495	21.9
Apr. 21	7.31	43	1	6	*1.065	29.8
Apr. 25	7.23	47	1	7	*.964	29.4
May 2	7.12	54	1	4	*1.458	32.8
May 6	6.97	58	1	4	*1.404	29.5
May 8	6.83	60	1	5	*.829	26.7
May 9	6.78	61	1	6	*.727	27.0
May 10	6.61	62	1	5	*1.348	30.9
May 11	6.49	63	1	6	*.969	27.7
May 12	6.72	64	1	7	*1.148	28.0
May 13	6.72	65	1	7	*.852	27.9
May 15	6.63	67	1	7	*.997	28.5
May 16	6.58	68	1	6	*.841	28.6
May 17	6.55	69	1	6	*.746	27.0
May 18	6.46	70	1	7	*.762	26.3
May 19	6.46	71	1	6	*.771	27.5
May 20	6.44	72	1	7	*.761	27.7
May 22	6.41	74	1	6	*.834	28.6
Oct. 18-19 <sup>3</sup>	6.22	<sup>4</sup> 93	1	24	<sup>5</sup> .650	23.0
Oct. 19-20	6.14		2	24	<sup>5</sup> .685	22.8
Oct. 20-21	6.07		3	24	*.648	23.8
Oct. 21-22	6.00		4	24	*.554	22.7
Oct. 22-23	5.92		5	24	*.617	23.2

\* Only starred values represent standard metabolism.

<sup>1</sup> At end of experiment python was put into exhibition cage for night, so it could drink water. It was found that python had shed its skin while in respiration chamber.

<sup>2</sup> Python placed in respiration chamber just before experiment began.

<sup>3</sup> About to shed skin on Oct. 12; finished late Oct. 16 or 17.

<sup>4</sup> Probably had not fed since night of July 17-18, 1916.

<sup>5</sup> Moderate activity in periods 1 and 2. Python put into respiration chamber at 10<sup>h</sup>30<sup>m</sup> a.m., Oct. 18; first period began at 11<sup>h</sup>55<sup>m</sup> a.m.

for snakes to go without food. Indeed, in Ditmars' paper <sup>1</sup> on the feeding of serpents, numerous cases are cited of snakes that fasted for several months. There is also the frequently cited instance of the large python at the New

<sup>1</sup> Ditmars, R. L., *Zoologica*, 1912, **1**, p. 197.

TABLE 51—*Metabolism of small Indian python—Fasting (Continued)*

Date	Body weight	Days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental Temperature
			No.	Length		
1916	kg.			hrs.	gm.	°C.
Oct. 27	5.91	102	1	3	<sup>6</sup> .799	22.7
Oct. 27			2	3	.569	22.2
Oct. 27			3	4	.580	22.2
Oct. 27			4	4	.476	25.7
Oct. 27-28			5	5	.686	23.8
Oct. 28			6	3	.620	22.6
Oct. 28	5.91		7	4	<sup>7</sup> .682	22.4
Oct. 28	5.89		8	3	* .577	21.9
Oct. 28			9	3	* .489	21.6
Oct. 28			10	4	* .522	21.4
Oct. 28-29			11	4	* .431	21.2
Oct. 29			12	6	* .424	21.8
Oct. 29	5.89		13	6	<sup>7</sup> .596	23.1
Oct. 30-31 <sup>8</sup>	5.88	105	1	24	* .265	16.6
Oct. 31-Nov. 1			2	24	* .282	17.2
Nov. 1-2			3	24	* .267	16.7
Nov. 2-3			4	24	* .301	16.5
Nov. 3-4	5.88		5	24	* .254	15.9
Dec. 5 <sup>9</sup>	6.00	16	1	3	1.263	22.7
Dec. 5			2	5	.899	22.5
Dec. 5-6			3	7	.710	22.3
Dec. 6			4	6	.649	22.2
Dec. 6			5	6	* .598	22.1
Dec. 6			6	8	* .608	22.0
Dec. 6-7			7	10	* .608	22.0
Dec. 7	6.00		8	6	* .570	22.0
1917						
Jan. 23 <sup>10</sup>	6.01	21	1	2	1.481	23.4
Jan. 23			2	5	1.123	23.9
Jan. 23-24			3	6	.880	23.2
Jan. 24			4	6	* .742	22.5
Jan. 24	6.01		5	7	* .681	22.6
Jan. 24	6.00		6	6	* .807	23.2
Jan. 24-25			7	6	* .759	23.1
Jan. 25			8	6	* .676	22.8
Jan. 25	6.00	22	9	6	* .666	22.6
Jan. 25	5.99		10	5	* .782	22.7
Jan. 25-26			11	9	* .671	22.6
Jan. 26			12	7	* .709	22.9
Jan. 26	5.99		13	6	* .728	22.9
Jan. 29 <sup>11</sup>	5.85	27	1	7	*1.311	29.6
Jan. 29-30			2	7	*1.275	28.8
Jan. 30			3	6	*1.326	29.5
Jan. 30	5.85		4	7	*1.354	30.3

<sup>6</sup> Python had been in exhibition cage since Oct. 23, and two unsuccessful attempts had been made to feed it. Put into respiration chamber at 9<sup>h</sup>40<sup>m</sup> a.m., Oct. 27; first period began at 10<sup>h</sup>45<sup>m</sup> a.m.

<sup>7</sup> Moderately active for a considerable time.

<sup>8</sup> Python in chamber overnight, Oct. 29-30; had not been disturbed for 20 hours.

<sup>9</sup> Python brought to laboratory Dec. 5; started to shed skin Nov. 29; had not quite finished Dec. 4.

<sup>10</sup> Python brought to laboratory probably Jan. 23.

<sup>11</sup> Python returned to reptile house at end of experiment on Jan. 26; put into respiration chamber at 12 noon, Jan. 29; first period began at 2<sup>h</sup>35<sup>m</sup> p.m.

TABLE 51—*Metabolism of small Indian python—Fasting (Continued)*

Date	Body weight	Days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environmental temperature
			No.	Length		
1917	kg.			hrs.	gm.	°C.
Jan. 31 <sup>12</sup>	5.82	29	1	5	* .306	17.7
Jan. 31–Feb. 1			2	22	* .315	17.5
Feb. 1–2			3	21	* .339	17.4
Feb. 2–3	(5.82)		4	26	* .358	17.0
Feb. 26 <sup>13</sup>	5.95	21	1	2	1.008	33.8
Feb. 26			2	2	1.392	35.3
Feb. 26			3	2	1.755	36.3
Feb. 26			4	3	2.284	37.0
Feb. 26			5	3	2.356	37.2
Feb. 26–27			6	3	2.307	37.3
Feb. 27			7	3	*2.485	37.4
Feb. 27			8	3	*2.662	38.6
Feb. 27			9	3	*2.717	38.8
Feb. 27			10	3	*2.737	37.3
Feb. 27	(5.95)		11	3	*2.743	37.5

<sup>12</sup> Python was cooled during night of Jan. 30–31 to a temperature of about 18° C.

<sup>13</sup> Python at 21° C. was put into warm respiration chamber at 10 a.m., Feb. 26; first period began 11<sup>h</sup>45<sup>m</sup> a.m.

York Zoological Park that fasted for 21 months<sup>1</sup> and the case reported by Martin<sup>2</sup> of a python that had not eaten for three years. Even when the small Indian python had been 149 days without food, comparison of its weight of 6.69 kg. with the initial weight of 7.43 kg. shows that as a result of 110 days further fasting (the first experiment began on the thirty-ninth day of fasting) the loss of weight was only 10 per cent of the initial body weight.

#### CONSTANCY IN STANDARD METABOLISM FROM PERIOD TO PERIOD

With a snake at a constant environmental temperature, in complete muscular and psychic repose, one would expect *a priori* (particularly in view of the remarkable absence of muscular activity that we usually found in all these snakes), relative constancy in the standard metabolism from period to period. Our first experiments with the small Indian python were not broken up into consecutive periods, so that until October 18, 1916, we have no suitable data for comparison. But from October 18 to 23, there are five periods, each of approximately 24 hours and at a relatively constant environmental temperature. The last three of these periods are starred as representing the standard metabolism. In the first two periods there was some activity, although with this particular python no great activity was recorded at any time. In the last three periods the carbon-dioxide production per kilogram of body weight per 24 hours was 0.648, 0.554 and 0.617 gram, respectively. In the next experiment, beginning October 27, the environmental temperature fluctuated in the first seven periods, but from the eighth to the twelfth period it was relatively constant, and we have

<sup>1</sup> Unpublished experiments of Dr. R. L. Ditmars at the New York Zoological Park. See, also, Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 377, 1927, p. 3.

<sup>2</sup> Martin, C. J., Lancet, 1930, p. 561.

five starred periods which show a reasonable uniformity in the carbon-dioxide production. In the thirteenth period the snake was moderately active, and the metabolism was consequently higher than under standard conditions, although the effect of activity is complicated by a rise in environmental temperature. At the low temperature of 16° to 17° C. on October 30 to November 4, a series of five periods indicates uniformity in metabolism. The same is true of periods 5 to 8 on December 6 to 7, and of periods 4 to 13 on January 24 to 26, 1917. At the high environmental temperature of nearly 30° C. on January 29-30, there is again uniformity in the successive periods, and on February 27 the constancy in the standard metabolism from period to period is particularly pronounced. The values on February 26 steadily increase, due to the fact that the environmental temperature increased and that the python prior to the experiment had been living at a lower temperature. These values are consequently not starred.

In general the consecutive periods under standard conditions show a relatively uniform carbon-dioxide production and point toward a uniformity in metabolism. If allowances are made for the extraordinary sensitivity of these serpents to rather slight temperature changes, which more than compensates for their usual muscular repose, and if allowances are made for the fact that the very small amounts of carbon dioxide produced, especially at the low temperatures, are occasionally disproportionate to the weights of the absorbing vessels used, there seems to be every evidence of a uniformity in the standard metabolism from period to period with this snake.

#### EFFECT OF AGITATION AND TRANSITIONS IN ENVIRONMENTAL TEMPERATURE

The influence of changes in temperature and the incomplete adjustment of the snake to the change in environment have already been discussed in the pages on the rectal temperature of snakes. In some of the experiments with the small Indian python, when it was studied too soon after being placed in the respiration chamber, it is possible that there were two disturbing factors, one the effect of handling and one the lag in temperature adjustment. On May 9, 10, 11, 12 and 15, 1916, there is definite evidence that the python was studied too soon after being placed inside the chamber, and undoubtedly we have here to deal with either one or, indeed, both of the above-mentioned factors. It is also clear that the adjustment to the new condition is always more rapid the higher the temperature. Thus on May 10, 1916, at an environmental temperature of 30.9° C., the carbon-dioxide production of 1.348 grams per kilogram of body weight per 24 hours during a 5-hour period is comparable to the standard values found on January 29-30, 1917, at essentially this temperature, although on May 10 the python had been placed in the chamber just before the experiment began. An interesting comparison of the effect of agitation resulting from placing the snake in the chamber just prior to the experiment, but complicated in a way by the natural result of a rising environmental temperature, is available in the experiment of February 26, 1917. In this experiment there was a rising environmental temperature and an increasing

carbon-dioxide production. In this case the python had been at a temperature of 21° C. for some time before the experiment, was placed in the warm chamber at 10.00 a.m., February 26, and the first experimental period began one and three-quarter hours later. Here the temperature effect

TABLE 52—*Standard heat production of small Indian python*

Date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq. m.	
1915-1917		<i>cal.</i>	<i>cal.</i>	°C.
Feb. 24-25	149	0.66	10.0	15.4
Jan. 31-Feb. 1	125	.57	8.6	16.5
Oct. 30-Nov. 4	107	.91	13.1	16.6
Jan. 31-Feb. 3	29	1.10	15.6	17.4
Feb. 21-23	146	.99	14.9	20.1
Jan. 25-26	119	1.16	17.7	20.5
Jan. 26-27	120	1.00	15.2	20.7
Feb. 17-18	142	.98	14.8	20.7
Oct. 28-29	103	1.63	23.4	21.6
Apr. 8-9	30	1.89	29.9	21.9
Apr. 18-19	40	1.65	25.9	21.9
Dec. 6-7	17	1.99	28.4	22.0
Jan. 24-26	22	2.41	34.4	22.8
Oct. 20-23	96	2.02	29.1	23.2
May 18	70	2.54	37.3	26.3
May 8	60	2.76	41.9	26.7
May 17	69	2.49	37.1	27.0
May 19	71	2.57	37.7	27.5
May 20	72	2.54	38.0	27.7
May 13	65	2.84	42.4	27.9
May 16	68	2.80	41.9	28.6
May 22	74	2.78	41.4	28.6
Feb. 2-3	127	2.05	31.0	29.0
Apr. 25	47	3.21	49.4	29.4
Feb. 4-5	129	2.16	32.6	29.5
May 6	58	4.68	70.9	29.5
Jan. 29-30	27	4.39	62.6	29.6
Apr. 21	43	3.55	55.2	29.8
May 2	54	4.86	75.2	32.8
Nov. 6	39	6.05	95.6	34.0
Feb. 8-9	133	3.12	47.8	34.0
Nov. 7	40	6.71	106.1	35.0
Nov. 9	42	5.66	89.5	35.0
Nov. 11	44	4.71	74.5	35.0
Feb. 14-15	139	3.52	53.4	35.0
Nov. 8	41	6.58	104.0	35.5
Nov. 13	46	4.76	75.2	35.5
Nov. 12	45	4.29	67.8	36.0
Feb. 27	22	8.89	129.0	37.9

<sup>1</sup> Derived from starred data in table 51.

was the predominant one, and the snake was making every effort to adjust itself to the environmental temperature, which ultimately reached 38° C. When this level was reached, the adjustment was made, for in the last four periods the metabolism was remarkably uniform.



## INFLUENCE OF ENVIRONMENTAL TEMPERATURE UPON STANDARD METABOLISM

On the assumption that the snake's rectal temperature tends to reach the temperature of the environment, although probably is appreciably below it, we may consider the influence of environmental temperature upon the standard metabolism. From table 51 it is obvious that the standard metabolism increases as the environmental temperature increases. If one compares only the last two experiments in the series, January 31 to February 3, 1917, inclusive, and February 26-27, 1917, inclusive, this fact is evident.

A more accurate study of this temperature effect can be made by plotting on a chart the values for the standard metabolism referred to the environmental temperature. Since, in the last analysis, our interest lies chiefly not in the carbon-dioxide production itself but in the energy transformations, we have computed the standard heat production from the standard carbon-dioxide production. These heat values, which are recorded in table 52, are derived only from those carbon-dioxide values in table 51 that are starred and represent average values for the different experiments and not period values. In table 52 are likewise recorded the calculations of the standard heat production per square meter of body surface per 24 hours, the body surface being computed according to the method described on page 147. These results, however, will not be analyzed until later (see page 215).

In figure 45 we have plotted for the small Indian python the calories produced per kilogram of body weight per 24 hours referred to environmental temperature, based upon the average values given in table 52. Against each plotted point has been written the number of days that the python had been without food. The tendency for a higher standard metabolism with a higher environmental temperature is seen immediately in figure 45. The highest heat production is at 38° C., which is the highest temperature, and the lowest is at 15° C., the lowest temperature. Inspection of this figure shows a number of plotted points that lie at a lower level than the other points, and it seems logical to suggest the projection of two lines or curves through these plotted points, one line definitely below the other. The lower plots are those obtained in the longer fasting period with this python. This fact is especially striking at the higher temperatures. It thus seems justifiable to sketch upon figure 45 two independent curves to represent the general trend of the standard metabolism with increasing environmental temperatures, the upper curve representing the shorter fasting series and the lower the longer fasting series. The lower curve lies materially below the upper throughout its whole length, indicating that the python is affected by prolonged fasting. The most pronounced features to be observed from these curves are the marked increase in metabolism with the rise in environmental temperature, and the fact that the same animal at the same environmental temperature shows a much lower metabolism after 120 days or more of fasting than after a shorter fast.

The scatter of the relatively few points obtained during the longer period of fasting is extraordinarily small. Indeed, practically all the points lie directly on the lower curve. In the shorter fasting period, on the contrary,

the scatter of the points is great, particularly between  $34^{\circ}$  and  $36^{\circ}$  C. Thus, at  $35^{\circ}$  C. the standard heat production on the fortieth day of fasting was 6.71 calories per kilogram of body weight per 24 hours, and at  $36^{\circ}$  C., on the forty-fifth day of fasting, it was 4.29 calories. This seems a wide distribution when compared with the almost insignificant scatter of the points about the lower curve for the long fasting period. The question naturally arises as to whether this distribution compares at all with that found, for example, with a group of warm-blooded animals or with children

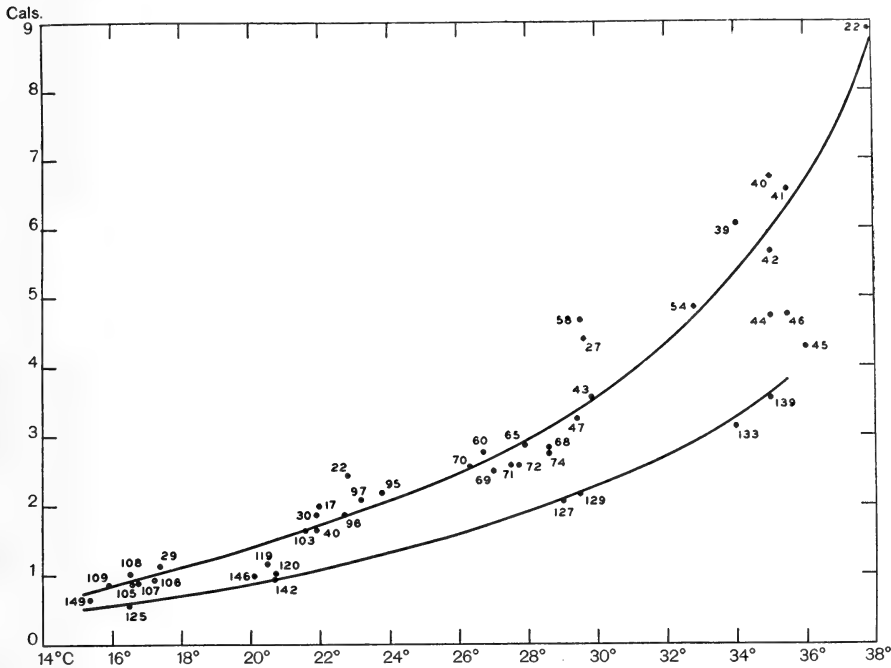


FIG. 45—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—SMALL INDIAN PYTHON.

Value against each plotted point indicates number of days that snake had been without food. Upper curve indicates trend of metabolism with increasing temperature during short fasts; lower curve shows trend during longer fasts.

or adults. This question will be considered later in this report (p. 234). At about  $29^{\circ}$  C. likewise there are two points that lie distinctly off the upper curve. One of them is for the fifty-eighth day of fasting, that is, on May 6, 1916. The other is after 27 days of fasting, on January 29-30, 1917. At this same temperature there are two other points at about 45 days of fasting that lie almost directly on the curve. It should be realized that, because of this scatter, the curve represents only a general average trend. A fasting interval of between 27 and 58 days is without significance with this snake, although the measurements were made at the same temperature. On the other hand, essentially the same heat production per kilogram of body weight is found, whether the metabolism is measured

at 29° or 36°. This of itself shows that we have to deal by no means solely with a thermally controlled reaction.

It may properly be argued that in the lower curve the snake was in a distinct state of undernutrition and had the characteristically lower metabolism noted with humans and other warm-blooded animals during undernutrition. With both warm- and cold-blooded animals undernutrition, apparently, causes a pronouncedly lower metabolism. During the period of prolonged fasting the python's average body weight was not far from 6.9 kg. During the short fasts it was about 7 kg. in the first part of the series and in the latter part of the series in 1917 it was nearer 5.9 kg. It is therefore impracticable to compare the results obtained with this python on the basis of difference in size alone, for there are three factors playing a rôle here—length of fasting, loss in body weight, and undernutrition—with the factor of undernutrition obviously playing the greater rôle.

The six points on figure 45 for 27, 44, 45, 46, 54 and 58 days of fasting, lying between 29° and 36° C. and between 4.39 and 4.86 calories, represent widely different stages of the python's existence. The values at the extreme right on the forty-fourth, forty-fifth and forty-sixth days of fasting were obtained in November 1915, when the snake weighed 7.43 kg. The values on the fifty-fourth and fifty-eighth days of fasting were obtained in May 1916, at a body weight of about 7 kg., and the value at 27 days of fasting was obtained in January 1917, when the snake was essentially at its minimum weight, 5.85 kg. It is obvious that the relationship between the state of nutrition, the actual length of the fast, the body weight of the animal, and the environmental temperature can not be simply solved, and any general conclusion drawn from these curves must be sufficiently conservative to recognize these aberrant values, for which we have no adequate explanation.

Finally, it must be considered that although figure 45 represents the heat production referred to the environmental temperature, undoubtedly we are not dealing here with the true body or rectal temperature, much less the true surface temperature. Our study of rectal and surface temperatures shows that these tend to be always a little below the environment, slightly below at the lower temperatures and noticeably below (to the extent of 2 degrees or more in the rectal temperature) at the higher temperatures. Lack of information concerning the exact rectal temperatures during these experiments with the small Indian python has made it unjustifiable to replot the heat values referred to the probable rectal temperatures, but obviously such replotting would give a somewhat steeper curve. Specifically, the highest value in the chart, 8.89<sup>1</sup> calories at 38° C., more properly belongs at a rectal temperature of 36°. At these high temperatures the skin temperature is noticeably cool, due to excessive vaporization of water, so that the average temperature of the body as a whole is probably somewhat below 36°, perhaps as low at 35° C.

With due consideration of all the seeming inconsistencies in figure 45, it can nevertheless be seen that there are three salient features brought out by these data, namely, that the metabolism of this small Indian python

<sup>1</sup>This was the last experiment made with this animal.

increases pronouncedly with the rise in environmental temperature, that it is lowered with prolonged fasting, and that the reaction in metabolism to changes in environmental temperature is of the same order of magnitude, irrespective of the length of the fast.

#### STANDARD METABOLISM OF A 5-METER PYTHON

With the idea of securing the greatest possible difference in the sizes of the various animals studied and particularly of securing the maximum sized snake, we were fortunately able, thanks to the kindness of Dr. Ditmars, to make a few measurements on a large Reticulated Python (*Python reticulatus*). This animal possessed the characteristic irritability and ferocity of the pythons, was difficult to handle, and the help of five members of the staff at the New York Zoological Park was required to make any measurements of it (fig. 40, p. 145). However, it was possible to secure measurements of the length and several girths, from which the surface area could be subsequently calculated. The python was put in a bag on March 20, 1916, placed on the balance and found to weigh 31.8 kg. Unfortunately, owing to the difficulties of handling this particular animal, a second weight was not obtainable, and we have only an imperfect record of the second weight obtained by difference, in that the snake and the men handling it were weighed on a large platform scale, and then the men were weighed immediately thereafter without the snake. This was on March 10, 1917, when the weight of the snake, admittedly only crudely determined, was 30.2 kg. Owing to the uncertainty in this second weight, we have used in all our calculations the weight of 31.8 kg. obtained on March 20, 1916. Although possibly in the 1917 series the python weighed somewhat (about 1 kg.) less than 31.8 kg., it was by no means obviously under-nourished, and one may consider that the error in assuming the initial weight of 31.8 kg. is not a great one.

The danger of exposing these animals to high environmental temperatures, coupled with the high cost of a snake of this size, restricted somewhat our experimental procedure, so that we felt constrained to expose this large python to a temperature not higher than 30° C. The temperature of the environment during the standard metabolism experiments, however, did range from as low as 16.2° to as high as 29.9° C., and there was one instance, on March 17, 1916, when the temperature during a period of transition did rise to as high as 34.4° C. This 5-meter python was measured in a large respiration chamber, the 908-liter chamber originally designed for the giant tortoise, but with a recessed cover reducing the residual volume to about 339 liters. The temperature control was by no means so perfect as with the smaller python, and we had to rely for a great deal of the time upon the temperature of the room itself.

The transfer of a python of this size from the exhibition cage into the respiration chamber called for much labor on the part of the men and especially caused a great deal of excitation and muscular movement on the part of the animal. Hence the effect of the previous agitation is seen clearly in the metabolism values for this large python, recorded in table 53. The first experiment on March 16-17 had been preceded by measure-

TABLE 53—*Metabolism of a 5-meter python—Fasting*  
(31.8 kg., Mar. 20, 1916; 30.2 kg., Mar. 10, 1917)

Date	Days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environ- mental tempera- ture
		No.	Length		
1916			<i>hrs.</i>	<i>gm.</i>	<i>°C.</i>
Mar. 16-17 <sup>1</sup>	182	1	2	3.736	29.5
		2	5	1.363	23.8
		3	5	.578	20.5
		4	5	.449	20.2
Mar. 17 <sup>2</sup>	183	1	1	.755	34.4
Mar. 18	184	1	3	* .385	22.6
		2	3	* .325	22.4
Mar. 18-19	184	1	15	* .294	20.6
Mar. 19	185	1	4	* .425	22.5
		2	2	* 1.378	22.4
Mar. 19-20	185	1	14	* .366	20.7
Mar. 20 <sup>4</sup>	186	1	1	3.532	22.1
		2	1	2.996	22.5
		3	1	1.925	23.2
		4	1	1.215	24.5
		5	1	.853	24.7
		6	2	* .564	23.8
		7	2	* .548	22.7
Mar. 20	186	1	13	* .388	21.5
1917					
Mar. 2 <sup>5</sup>	213	1	1	5.525	23.2
		2	2	1.634	23.0
		3	2	.826	22.7
		4	2	.589	22.5
		5	2	* .487	22.8
		6	2	* .558	23.2
Mar. 3	214	1	2	* .411	24.1
		2	2	* .381	23.9
		3	3	* .459	23.9
		4	2	* .442	24.2
		5	2	* .411	23.9
		6	2	.679	23.1
Mar. 4	215	1	2	* .238	17.5
		2	2	* .260	17.2
		3	2	* .317	16.9
		4	2	* .285	17.1
		5	2	.653	17.4
Mar. 5	216	1	2	.306	16.0
		2	2	.339	16.1
		3	2	.362	16.4
		4	2	* .264	16.5
		5	3	* .306	16.2
		6	2	* .252	16.2

TABLE 53—*Metabolism of a 5-meter python—Fasting*  
(Continued)  
(31.8 kg., Mar. 20, 1916; 30.2 kg., Mar. 10, 1917)

Date	Days fasting	Period		CO <sub>2</sub> per kg. per 24 hours	Environ- mental tempera- ture
		No.	Length		
1917 Mar. 6	217	1	hrs. 2	gm. 1.106	°C. 24.5
		2	3	1.099	25.5
		3	2	1.075	27.0
		4	3	* .909	27.4
		5	2	* .873	27.6
Mar. 7	218	1	1	* .834	28.7
		2	1	* .871	29.5
		3	1	*1.093	29.5
		4	1	* .815	29.3
		5	1	*1.017	29.5
		6	1	*1.079	29.8
		7	1	*1.253	29.9
		8	1	*1.004	29.7
Mar. 8	219	1	2	* .249	20.0
		2	2	* .314	19.5
		3	4	* .372	19.0
Mar. 9	220	1	2	* .403	21.4
		2	2	* .408	22.7
		3	1	* .583	23.1
		4	2	* .439	23.3
		5	2	* .462	23.5
Mar. 10	221	1	1	.657	26.2
		2	1	* .551	26.1
		3	1	* .558	26.2

\* Only starred values represent standard metabolism.

<sup>1</sup> Girth measurements made before experiment of Mar. 16.

<sup>2</sup> Less than 5 hrs., 30 mins., between temperatures as low as 20° C. at end of experiment on Mar. 16-17 and the high temperature of Mar. 17.

<sup>3</sup> Very active throughout second period.

<sup>4</sup> Girth measurements made before experiment of March 20.

<sup>5</sup> Python taken from cage in reptile house 25 minutes before this experiment and exposed to outdoor temperature of 0.5° C. for 10 minutes during its removal from reptile house to primate house, where respiration chamber was installed.

ments of length and girths. The animal was considerably agitated by this procedure, and we would expect, therefore, a continually decreasing carbon-dioxide production per kilogram of body weight per 24 hours in the successive periods, but the results are complicated by the fact that there was simultaneously a pronounced fall in the temperature of the environment. For these reasons it was impossible to use any of the period values in this first experiment for true comparison of the relationship between temperature of the environment and the metabolism. The next experiment on March 17 was complicated by the fact that the python had been at a temperature as low as 20° C. prior to the period of observation. The temperature of the chamber was increased and the experiment,

which continued only one hour, was begun less than 5½ hours after the python had come out of a 20° environment. We believe that the carbon-dioxide value obtained is not truly representative of the metabolism at 34.4° C., which was the temperature actually used on that particular day, although it was never repeated thereafter. It will be noted that in later experiments in which the python was measured at temperatures between 27° and 30° C. the carbon-dioxide production was considerably higher than that found on March 17, 1916. Hence in this short time of 5½ hours the python had by no means succeeded in reaching a body temperature comparable to a chamber environment of 34.4° C.

The first values that we feel confident can be used for comparison are those of March 18, 1916, when the python was at 22.5° C. On this date two well-agreeing periods were obtained. From then on there are a number of starred values in table 53, all of which are used subsequently in studying the relationship between the environmental temperature and the standard metabolism (fig. 46, p. 206). In the latter part of the experiment on March 19, 1916, there was pronounced activity. In the first period, a starred period, the carbon-dioxide production was only 0.425 gram per kilogram of body weight per 24 hours. In the second period, during which the python was very active, the metabolism had increased over 300 per cent. This is a percentage increase due to activity wholly outside our experience with warm-blooded animals inside a respiration chamber. It is equivalent to the increase in the metabolism of a man walking on a road compared with that of a man in complete muscular repose.

On March 20, 1916, a series of girth measurements preceded the experiment, and the pronounced effect of agitation is shown in the high carbon-dioxide production at the relatively low temperature. Here is clear evidence of the effect not of temperature but of agitation. The high values gradually decreased until standard values were obtained in the sixth and seventh periods at an average temperature of not far from 23° C. The large python was fed on March 23, 1916, and several times thereafter, the last date of feeding prior to the 1917 series of experiments being August 1, 1916.

On March 2, 1917, after fasting 213 days, the python was given a wholly unusual experience, in that 25 minutes before the first experimental period began it was taken out of the cage in the reptile house, carried outdoors to a temperature of 0.5° C. for ten minutes, and then taken to the primate house, where the respiration chamber had been set up. During these ten minutes, as has already been pointed out (p. 53), the rectal and the mouth temperature fell approximately 2° C., being 24.3° and 24.4°, respectively, upon arrival at the primate house. The high metabolism, therefore, incidental to this experience is undoubtedly due not to a previously high temperature but to the muscular activity and agitation, for the environmental temperature averaged nearly 23°, not far from the rectal temperature. This high metabolism gradually falls off as the python becomes calm, and the fifth and sixth periods give results that can be considered as standard. In further experiments with this python, precaution was taken to avoid unnecessary transitions or activity, the animal remaining quiet for most

of the time and not being removed from the chamber. Hence in the later experiments one notices the absence of great changes in metabolism, except where the environmental temperature has been raised or lowered. The number of starred periods again shows clearly the regularity of metabolism from period to period under standard conditions.

With this large python, therefore, we have evidence of the influence of activity, as on March 19, 1916, and the influence of agitation or previous handling, as on March 16-17, 1916, March 20, 1916, and particularly March 2, 1917. The results also indicate the regularity of metabolism under constant conditions, and comparison of the starred values shows that at high

TABLE 54—Standard heat production of a 5-meter python

Date	Days fasting	Heat produced per 24 hours <sup>1</sup>		Environmental temperature
		Per kg.	Per sq.m. <sup>2</sup>	
1916-1917		<i>cal.</i>	<i>cal.</i>	°C.
Mar. 5	216	.91	20.1	16.3
Mar. 4	215	.92	20.3	17.2
Mar. 8	219	1.04	23.0	19.5
Mar. 18-19	184	.98	21.6	20.6
Mar. 19-20	185	1.22	26.9	20.7
Mar. 20-21	186	1.29	28.5	21.5
Mar. 18	184	1.18	26.1	22.5
Mar. 19	185	1.42	31.4	22.5
Mar. 9	220	1.53	33.8	22.8
Mar. 2	213	1.74	38.4	23.0
Mar. 20	186	1.86	41.1	23.3
Mar. 3	214	1.40	30.9	24.0
Mar. 10	221	1.85	40.9	26.2
Mar. 6	217	2.97	65.6	27.5
Mar. 7	218	3.32	73.3	29.5

<sup>1</sup> Derived from starred data in table 53.

<sup>2</sup> Based on actually measured surface area of 1.44 sq. m.

environmental temperatures there is a high standard metabolism and at low temperatures a low metabolism.

The relationship between the environmental temperature and the standard metabolism can best be studied by plotting the data upon a chart. The average standard heat production for each experiment has therefore been calculated, by multiplying the starred carbon-dioxide values in table 53 by 3.325 and averaging the starred period values for each experiment. The results of such calculations are given in table 54 for the average 24-hour heat production both per kilogram of body weight and (for use in subsequent discussion, p. 217) per square meter of body surface. In figure 46 are plotted the values for the standard heat production per kilogram of body weight referred to the environmental temperature. This figure enables a study of the reaction of this large python to environmental temperature, although again it should be remembered that undoubtedly the true temperature of the rectum was slightly below that of the environment at the lower



temperatures and much below (about  $2^{\circ}$  C.) at the higher temperatures. A curve has been sketched through these points to represent the general trend of the metabolism. This shows that the scatter of the points is not abnormally great. It is to be regretted that more metabolism measurements at the higher temperatures could not have been obtained, but, as already pointed out, the possible danger to the costly python made such measurements impracticable.

According to this curve in figure 46 the average standard heat production per kilogram of body weight per 24 hours at  $17^{\circ}$  C. is 0.9 calorie and at  $27^{\circ}$  it is 2.4 calories. Here the heat production is increased 270 per cent by the

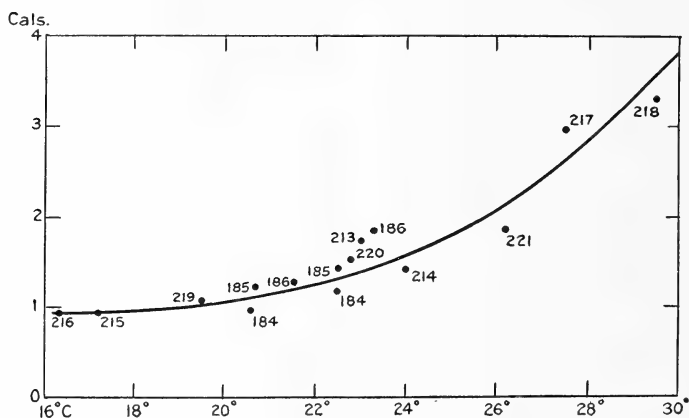


FIG. 46—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—5-METER PYTHON.

Value against each plotted point indicates number of days that snake had been without food.

$10^{\circ}$  rise in temperature. At  $20^{\circ}$  the projected curve cuts the ordinates for heat at 1.05 calories and at  $30^{\circ}$  at 3.75 calories. Here the increase in heat production is materially greater, 357 per cent. The exact direction of the curve at this higher temperature, however, is somewhat uncertain, owing to the absence of more measurements at this level. The quantitative comparison of the metabolism of this large python and that of the small Indian python is left for a subsequent chapter (p. 213).

#### STANDARD METABOLISM OF THE 1931 PYTHON

In January 1931, the Nutrition Laboratory secured a 5-kg. python with which to make further studies of the problems that had arisen in its research on the physiology of snakes. Through the kindness of Dr. Raymond L. Ditmars, this python was kept for a few days after its purchase at the New York Zoological Park and was fed two rabbits on January 6. The animal was in moderately good condition, although not fat. It had been shipped from Calcutta to New York ten months before the Nutrition Laboratory purchased it, and had been fed guinea-pigs or rabbits about once

every two months, but apparently had not been handled at all. Dr. Ditmars thought it might be seven or eight years old. It was of the species *Python molurus*, sometimes called "javelin-headed python" because on the back of the head there is a mark noticeably like a javelin. A few observations on the rectal temperature of this python during the digestive stage were secured in the New York Zoological Park, and on January 9 the animal was brought to the Nutrition Laboratory in Boston.

The detailed results of the respiration experiments that were carried out with this python between January 14 and February 26, 1931, are recorded in table 55. The environmental temperature was purposely altered in the different experiments, in order to study the influence of this factor. One digestive cycle was also studied, the python being fed two guinea-pigs at 5 p.m. on January 24, following a respiration experiment on that day. The temperature recorded in the first column of the table represents the rectal temperature determined at the end of the metabolism experiment. The environmental temperature given in the last column is that which prevailed inside the respiration chamber during the experiment. The heat production has been computed from the oxygen consumption at the caloric value indicated by the actually determined respiratory quotient. In those instances when the respiratory quotient was below 0.70, the caloric value of oxygen has been assumed to be that for a quotient of 0.70. The data for the respiratory quotients themselves will be discussed in detail subsequently (see pages 409 to 418). The asterisks against the oxygen values indicate, as usual, those periods when the metabolism was measured under "standard conditions." The unstarred oxygen values represent periods complicated by digestion, activity, or transitions in environmental temperature. The "standard" heat values correspond to the starred oxygen values. They have not been starred. The values enclosed in parentheses on January 27, January 29 and February 3 have not been included in calculating the average metabolism on these dates for record in table 84 (p. 296).

The average values for each day when the metabolism was measured under standard conditions are given in table 56. This table includes columns for the temperature of the air inside the respiration chamber during the experiment (called the "line temperature"), the rectal temperature taken at the end of the various respiration experiments, and the temperature of the respiration chamber at the time the rectal temperature was secured, read on a thermometer resting on the bottom of the chamber. From this table, arranged chronologically as it is, it is difficult to see the relationship between the standard metabolism and the environmental temperature. This is best shown by a chart (fig. 47) in which the values for the standard heat production per kilogram of body weight per 24 hours have been plotted with reference to the environmental temperature. At temperatures of 25° and above the heat values have been plotted with respect to the rectal temperature of the snake, when known, and at temperatures below 25° with respect to the environmental temperature, that is, the temperature prevailing inside the respiration chamber during the experiment. At the lower temperatures the differences between the rectal and the environmental temperatures are relatively small, but at the higher

TABLE 55—Summary of gaseous metabolism measurements on 1931 python

Date, days fasting, weight, and rectal temperature	Length of period	R. Q.	Per kg. per 24 hours		Heat produced per 24 hours		Environ- mental tempera- ture
			O <sub>2</sub>	H <sub>2</sub> O	Per kg.	Per sq.m.	
1931	<i>mins.</i>		<i>c.c.</i>	<i>gm.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
Jan. 14	95	0.88	* 541	2.48	2.65	37.4	26.0
8 days	90	.75	* 613	2.73	2.91	41.1	26.0
5.5 kg.	90	.72	* 526	2.94	2.47	34.9	25.4
Jan. 15 <sup>1</sup>	120	.66	* 302	1.88	1.42	20.0	22.1
9 days	120	.62	* 460	2.84	2.16	30.5	22.2
5.5 kg.							
22.7° C.							
Jan. 16	120	.66	* 404	2.63	1.89	26.7	24.1
10 days	120	.70	* 364	2.03	1.71	24.1	24.7
5.5 kg.	120	.67	* 371	2.27	1.74	24.6	24.8
Jan. 17	90	.65	* 351	1.91	1.64	23.1	23.9
11 days	105	.66	* 349	1.95	1.64	23.1	24.5
5.5 kg.	90	.72	* 313	1.95	1.47	20.7	24.6
24.7° C.	100	.70	* 332	1.64	1.56	22.0	24.6
Jan. 19 <sup>2</sup>	180	.59	* 206	1.33	.97	13.7	18.5
13 days	180	.59	* 179	1.37	.84	11.8	17.9
5.5 kg.							
Jan. 20 <sup>3</sup>	120	.60	* 228	1.71	1.07	15.0	20.0
14 days	120	.60	158	1.39	.74	10.4	17.6
5.4 kg.	100	.57	146	1.37	.68	9.6	16.6
14.3° C.							
Jan. 21	60	.69	* 641	2.98	3.00	42.2	31.8
15 days	50	.73	* 637	3.23	3.00	42.2	31.7
5.4 kg.	50	.71	* 632	3.56	2.96	41.6	31.6
31.0° C.	50	.65	* 688	3.96	3.22	45.2	31.5
	60	.70	* 677	4.61	3.17	44.5	31.3
Jan. 22	75	.66	* 604	4.26	2.83	39.7	31.3
16 days	75	.68	* 688	5.62	3.22	45.2	31.5
5.4 kg.	75	.73	* 641	5.53	3.02	42.4	31.4
31.4° C.	75	.70	* 656	4.45	3.07	43.1	31.3
Jan. 23	77	.68	* 347	2.33	1.63	22.9	24.9
17 days	75	.69	* 339	2.31	1.59	22.3	24.9
5.4 kg.	90	.69	* 340	2.50	1.59	22.3	25.0
24.7° C.	90	.70	* 345	2.61	1.62	22.7	24.9
Jan. 24 <sup>4</sup>	90	.72	* 386	4.39	1.81	25.4	25.3
18 days	110	.52	<sup>5</sup> 960	4.33	4.50	63.2	25.3
5.4 kg.	105	.97	<sup>5</sup> 662	4.73	3.32	46.6	25.2
25.1° C.							
Jan. 27 <sup>6</sup>	4	.72	4497	....	21.14	315.5	32.0
3 days	4	.73	(3704)	....	(17.46)	(260.6)	(31.9)
6.5 kg.	2.5	.72	4524	76.28	21.28	317.6	32.0
35.6° C.	2.4	.71	4595	4.21	21.55	321.6	31.9
	2.4	.71	4427	7.62	20.76	309.8	31.8

\* Only starred values represent standard metabolism.

<sup>1</sup> Snake not removed from chamber after experiment of Jan. 14. In an environment of 22° overnight, Jan. 14-15.

<sup>2</sup> Snake at 18° for 24 hours preceding experiment of Jan. 19.

<sup>3</sup> Laboratory room was very warm (25° or 26°), and it was difficult to control temperature of chamber.

<sup>4</sup> Python in box with wire partitions, to prevent coiling and to expose as much of body surface as possible. Jan. 24, after respiration experiment, python ate 2 guinea-pigs.

<sup>5</sup> Active.

TABLE 55—Summary of gaseous metabolism measurements on 1931 python  
(Continued)

Date, days fasting, weight, and rectal temperature	Length of period	R. Q.	Per kg. per 24 hours		Heat produced 24 hours		Environ- mental tempera- ture
			O <sub>2</sub>	H <sub>2</sub> O	Per kg.	Per sq.m.	
1931	<i>mins.</i>		<i>c.c.</i>	<i>gm.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
Jan. 29 <sup>6</sup>	3.4	0.59	(2563)	(4.09)	(12.01)	(179.2)	(31.8)
5 days	3.3	.62	(2556)	(5.14)	(11.98)	(178.8)	(31.6)
6.5 kg.	6.5	.56	3491	4.29	16.36	244.2	31.2
	5.6	.62	4287	....	20.09	299.8	31.2
	5.9	.58	3445	....	16.14	240.9	31.1
	5.8	.55	3802	....	17.82	266.0	31.1
Jan. 30 <sup>6</sup>	6.8	.75	1524	4.24	7.22	108.2	31.1
6 days	6.4	.73	1667	4.15	7.86	117.8	31.2
6.6 kg.	6.4	.74	1608	4.42	7.60	113.9	31.1
	7.1	.72	1700	4.43	7.99	119.8	30.9
				4.22			
Jan. 31 <sup>6</sup>	7.4	.75	1831	73.79	8.68	129.8	33.2
7 days	7.4	.72	2103	4.15	9.89	147.9	33.0
6.5 kg.	7.6	.75	1947	6.53	9.23	138.1	32.9
34.0° C.	7.9	.70	1788	5.38	8.38	125.3	32.5
				4.64			
Feb. 2 <sup>6</sup>	8.6	.66	1355	72.79	6.35	95.5	30.7
9 days <sup>8</sup>	7.8	.80	1162	3.11	5.58	83.9	31.9
6.6 kg.	8.8	.76	1099	2.88	5.22	78.5	31.1
32.5° C.	8.7	.75	1223	2.91	5.80	87.2	30.0
				3.44			
				3.08			
Feb. 3 <sup>6</sup>	8.0	.79	(1175)	(3.36)	(5.63)	(83.4)	(31.5)
10 days	9.5	.75	863	2.82	4.09	60.6	30.8
6.4 kg.	9.3	.75	834	3.19	3.95	58.5	32.0
	9.8	.75	650	2.98	3.08	45.6	31.5
Feb. 4	60	.67	*1450	3.51	6.79	100.4	36.8
11 days	60	.71	*1288	2.83	6.04	89.3	36.3
6.3 kg.	60	.70	*1264	2.93	5.92	87.5	35.3
38.7° C.	61	.70	*1787	3.33	8.37	123.8	34.7
	60	.69	*1518	3.08	7.11	105.2	34.0
Feb. 6	90	.66	* 720	1.29	3.37	49.9	31.6
13 days	90	.72	* 529	.92	2.49	36.8	31.4
6.3 kg.	60	.69	* 677	2.06	3.17	46.9	31.4
33.1° C.	60	.72	* 463	1.90	2.18	32.3	30.8
Feb. 9	120	.60	* 147	.84	.69	10.2	18.1
16 days	120	.62	* 149	.44	.70	10.3	17.9
6.2 kg.	105	.60	* 129	.60	.60	8.8	17.9
Feb. 10	120	.62	* 160	1.05	.75	11.0	18.7
17 days	120	.61	* 152	.61	.71	10.4	18.7
6.2 kg.	120	.63	* 154	.55	.72	10.6	18.9
18.9° C.							
Feb. 12	180	.60	* 174	.96	.82	12.1	17.8
19 days	120	.63	* 142	....	.67	9.9	17.5
6.2 kg.	180	.62	* 155	1.21	.73	10.7	17.6

<sup>6</sup> Digestive period.<sup>7</sup> Measurements of water vapor made at end of oxygen measurements.<sup>8</sup> Python shed its skin between Jan. 31 and Feb. 2.

TABLE 55—*Summary of gaseous metabolism measurements on 1931 python (Continued)*

Date, days fasting, weight, and rectal temperature	Length of period	R. Q.	Per kg. per 24 hours		Heat produced per 24 hours		Environ- mental tempera- ture
			O <sub>2</sub>	H <sub>2</sub> O	Per kg.	Per sq.m.	
1931	<i>mins.</i>		<i>c.c.</i>	<i>gm.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
Feb. 13	60	0.58	170	....	.80	11.8	17.8
20 days	120	.60	222	.88	1.04	15.3	17.9
6.2 kg.	60	.65	341	.25	1.60	23.5	29.7
30.6° C.	60	.79	260	.39	1.25	18.4	31.2
	60	.84	430	1.20	2.09	30.7	30.9
	60	.76	393	1.27	1.87	27.5	30.7
	72	.64	* 532	1.43	2.49	36.6	30.5
	60	.74	* 707	1.85	3.34	49.1	31.7
	60	.80	* 572	1.92	2.75	40.4	32.7
	60	.70	* 686	1.68	3.21	47.2	32.3
	67	.65	* 648	1.55	3.04	44.7	32.1
	60	.71	892	3.06	4.18	61.4	32.0
Feb. 16 <sup>a</sup>	270	.71	* 377	....	1.77	25.3	21.7
23 days							
5.7 kg.							
Feb. 17 <sup>a</sup>	155	.73	* 786	....	3.71	53.1	30.2
24 days							
5.7 kg.							
Feb. 18	30	.72	* 561	4.45	2.64	37.7	29.2
25 days	35	.75	* 487	2.18	2.31	33.0	29.3
5.7 kg.	40	.76	* 509	2.26	2.42	34.5	29.1
29.4° C.	45	.76	* 481	1.94	2.29	32.7	28.9
	45	.71	* 560	2.39	2.63	37.5	28.8
Feb. 19	30	.72	* 606	4.04	2.85	40.9	32.5
26 days	31	.69	* 661	3.85	3.10	44.5	32.7
5.8 kg.	30	.68	* 685	4.04	3.21	46.1	32.1
33.1° C.	40	.68	* 759	3.20	3.56	51.1	32.3
Feb. 20	50	.66	* 986	5.66	4.62	66.1	34.8
27 days	50	.67	* 987	4.81	4.63	66.3	35.2
5.7 kg.	50	.68	* 966	5.65	4.53	64.8	34.9
36.2° C.	45	.69	* 998	4.96	4.68	67.0	34.8
	55	.69	* 962	5.23	4.51	64.6	35.2
Feb. 21	50	.64	* 792	4.23	3.71	53.2	35.7
28 days	50	.68	* 885	4.10	4.15	59.5	36.1
5.8 kg.	50	.72	* 826	4.45	3.88	55.6	35.9
36.1° C.	50	.73	* 860	3.97	4.05	58.1	36.2
	60	.72	* 901	4.67	4.24	60.8	36.4
	50	.72	* 897	5.45	4.22	60.5	36.0
Feb. 24	50	.76	* 964	6.51	4.58	66.0	37.8
31 days	50	.75	* 946	5.63	4.48	64.5	38.0
5.8 kg.	50	.74	* 937	6.31	4.43	63.8	38.2
37.9° C.	50	.72	* 978	6.11	4.60	66.3	38.4
	55	.72	* 987	6.36	4.64	66.8	37.9
Feb. 26	60	.55	* 116	.40	0.54	7.7	17.4
33 days	80	.60	* 184	.75	.86	12.3	17.0
5.8 kg.	105	.56	* 210	.56	.98	14.1	17.8
17.3° C.							

<sup>a</sup> Calorimeter experiment.

temperatures the rectal temperature is a fraction of a degree lower than the environmental temperature. Hence it seems advisable at the higher levels to plot the values with reference to the rectal temperature and to indicate them by crosses. The dots represent values plotted with respect to the environmental temperature, and those dots and crosses surrounded by circles indicate the experiments made up to and including January 24, that

TABLE 56—*Standard metabolism of 1931 python*

Date	Days fast-ing	Body weight	Period		R. Q.	O <sub>2</sub> per kg. per 24 hours	Heat produced per 24 hours		Temperature		
			Total No.	Length (avg.)			Per kg.	Per sq.m.	Line	Rectal	Chamber bottom
1931		<i>gm.</i>		<i>mins.</i>		<i>c.c.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>	<i>°C.</i>	<i>°C.</i>
Jan. 14	8	5500	3	92	0.78	560	2.68	37.8	25.8	....	....
Jan. 15	9	5493	2	120	.64	381	1.79	25.3	22.2	22.7	22.1
Jan. 16	10	5486	3	120	.68	380	1.78	25.1	24.5	....	....
Jan. 17	11	5479	4	96	.68	336	1.58	22.2	24.4	24.7	24.8
Jan. 19	13	5455	2	180	.59	193	.91	12.8	18.2	....	....
Jan. 20	14	5430	1	120	.60	228	1.07	15.0	20.0	14.3	12.8
Jan. 21	15	5415	5	54	.70	655	3.07	43.1	31.6	31.0	31.3
Jan. 22	16	5415	4	75	.69	647	3.04	42.6	31.4	31.4	31.8
Jan. 23	17	5415	4	83	.69	343	1.61	22.6	24.9	24.7	24.7
Jan. 24	18	5400	1	90	.72	386	1.81	25.4	25.3	25.1	25.8
Feb. 4	11	6320	5	60	.69	1461	6.85	101.2	35.4	38.7	37.4
Feb. 6	13	6325	4	75	.70	597	2.80	41.5	31.3	33.1	31.3
Feb. 9	16	6237	3	115	.61	142	.66	9.8	18.0	....	....
Feb. 10	17	6230	3	120	.62	155	.73	10.7	18.8	18.9	18.5
Feb. 12	19	6209	3	160	.62	157	.74	10.9	17.6	....	17.6
Feb. 13	20	6200	5	64	.71	629	2.97	43.6	31.9	30.6	31.6
Feb. 16	23	5730	1	270	.71	377	1.77	25.3	21.7	....	....
Feb. 17	24	5713	1	155	.73	786	3.71	53.1	30.2	....	....
Feb. 18	25	5670	5	39	.74	520	2.46	35.1	29.1	29.4	31.2
Feb. 19	26	5783	4	33	.69	678	3.18	45.7	32.4	33.1	33.7
Feb. 20	27	5727	5	50	.68	980	4.59	65.8	35.0	36.2	35.2
Feb. 21	28	5755	6	52	.70	860	4.04	58.0	36.1	36.1	36.1
Feb. 24	31	5840	5	51	.74	962	4.55	65.5	38.1	37.9	39.8
Feb. 26	33	5755	3	82	.57	170	.79	11.4	17.4	17.3	15.8

is, prior to the digestion experiment. This distinction was made in the belief that possibly the metabolism measurements subsequent to January 24 might have been influenced by the food and that on February 4, or 11 days after food, there might still have been some digestive activity. A curve has been sketched through these plotted points to indicate the approximate trend of the metabolism, and it can be seen that, as is common with all these cold-blooded animals, the metabolism increased with the increase in temperature. The highest temperature at which the metabolism was measured was 38.7°, when the heat production was nearly 7 calories per kilogram of body weight per 24 hours. At 18° the heat production in general averages about 0.80 calorie. Although the plotted points deviate considerably from the general line, on the whole the trend of the metabolism seems to be well shown by the nature of the curve.

In this series of experiments with the 1931 python there was a rather considerable change in body weight between the experiments made prior

to January 24 and those after January 24. In the series from February 4 to 13, inclusive, the snake weighed on the average 6.3 kg., whereas in the experiments prior to February 4 it weighed 5.4 kg. The difference in weight is obviously due to the deposition of body material as a result of the ingestion of two guinea-pigs on the afternoon of January 24. The difference in body weight is presumably in part compensated by computing the metabolism per unit of body weight, and it is worthy of note that the results obtained after January 24, that is, at the higher body weight, are not at a remarkably different level from that of the results obtained prior

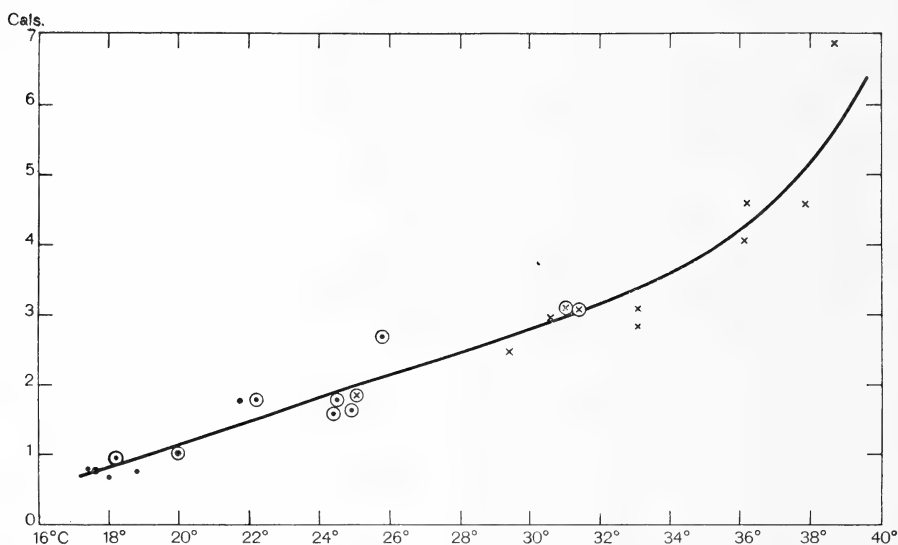


FIG. 47—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL OR RECTAL TEMPERATURE—1931 PYTHON.

Dots enclosed in circles represent values obtained before digestion period and plotted with reference to environmental temperature. Dots not enclosed in circles represent values obtained after the digestion period and plotted with reference to environmental temperature. Crosses enclosed in circles represent values obtained before digestion period and plotted with reference to rectal temperature. Crosses not enclosed in circles represent values obtained after digestion period and plotted with reference to rectal temperature.

to the ingestion of food. Indeed, the points enclosed in the circles, which represent the values secured before January 24, follow the curve nearly as well as do the points without circles, thus showing that there is no difference in the standard heat production even with this rather considerable variation in body weight, when the difference in weight is equalized by computing the heat production per unit of body weight.

*Practicability of using the python for laboratory experimentation*—The Nutrition Laboratory's satisfactory experience in using the 1931 python for metabolism experiments leads us to point out the practicability of making further studies with the larger snakes. We found, for example, that an 8- or 9-foot python costs (in New York, January 1931) \$30 or the equivalent of the cost of twenty guinea-pigs, and the expense of feeding it is very

little. With the use of a suitable metabolism cage it is possible to separate the urine and feces of the snake so that analyses can be made of the composition of the excreta, regarding which little is known. Neither the python nor the boa is poisonous. They frequently remain for a long time in the animal dealer's collection before they are purchased. They are accustomed to much handling, will rarely bite, and if one wears an ordinary coat and good automobile gauntlets, the danger from biting is reduced to practically nothing. If desired, a blanket can first be put over the snake, and the investigator can then reach for the neck just back of the head without attracting the snake's attention. One man or at the most two men can easily handle a 3-meter snake. After a few days the snakes become more accustomed to handling, give less and less trouble, and, indeed, they have been handled in the Nutrition Laboratory by one person. It would appear, therefore, as if it is perfectly feasible to study the intermediary metabolism of these large cold-blooded animals—a study that has been too long neglected.

#### COMPARISON OF STANDARD METABOLISM OF SNAKES OF SAME SPECIES

##### COMPARISON OF HEAT PRODUCTION OF PYTHONS

##### HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT

The three pythons studied by us were characterized by a great difference in weight, the so-called "small Indian python" weighing on the average 6.5 kg. throughout the period of study, the 1931 python from 5.5 to 6.5 kg., and the large 5-meter python 31.8 kg. This latter animal comes under the head of the giant pythons, although it was exceeded in size by some of the other specimens at the New York Zoological Park. As one of the largest snakes the metabolism of which has ever been studied, it is of unusual interest in comparison with the smaller pythons. The simplest method for comparison is on the basis of the standard heat production per kilogram of body weight, for obviously the larger mass of the large python would produce a greater total heat than that of the smaller pythons. The heat production of these three animals has already been discussed separately on this basis, by means of tables and charts. A direct comparison of the three pythons is best made by plotting on one chart the general curves representing the trend of the metabolism of these snakes with increasing temperature. One of the first problems that presents itself in making such a comparison is that for the small Indian python there are two curves at distinctly different levels, since in one series of observations this python had fasted much longer than in the other series and the metabolism was consequently lower. In general, the small Indian python had fasted not far from 125 to 150 days when the data for the lower curve in figure 45 (p. 199) were obtained. On the other hand, the large python had fasted somewhat longer, from 182 to 221 days, when the values for the curve in figure 46 (p. 206) were obtained. Since it appeared from the comparison of the standard metabolism values for the small Indian python that the more prolonged fasting resulted in a lower heat production per kilogram of body weight, one would expect that the large python, having



fasted much longer, would have a low metabolism when compared with that of the small Indian python.

The general curve representing the heat production per kilogram of body weight of the large python referred to environmental temperature, the two curves for the small python at the two different stages of fasting, and the curve for the 1931 python, have been reproduced in figure 48, taken directly from figures 45, 46 and 47 (pages 199, 206, and 212). The curve for the large python (the short dashed line) lies for the greater part of its length below the curve for the 1931 python and midway between the two curves representing the standard metabolism of the small Indian python,

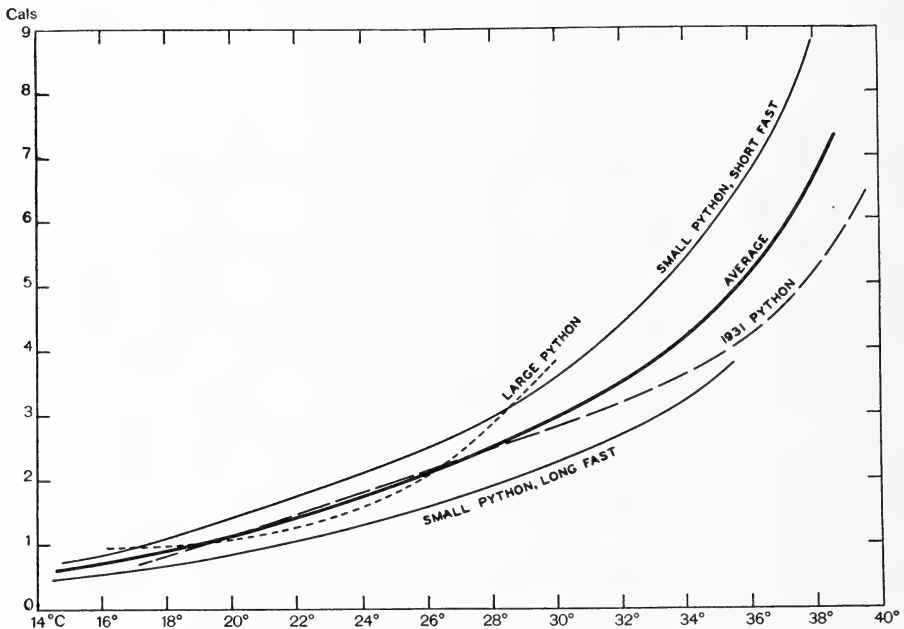


FIG. 48—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO TEMPERATURE—ALL PYTHONS.

but between 28° and 30° it rises above the curve for the short fasting series with this small python. The curve for the large python lies the entire time above the curve for the long fasting period with the small python, and yet the large python fasted a longer time than did the small python. If it were permissible to correct the curve for the large python so that it would represent the same length of fasting as the curve for the small Indian python during its short period of fasting, the curve for the large python would then lie measurably above that for the short fast of the small python. The curve for the 1931 python lies about midway between the two curves for the small Indian python. On the basis of heat production per kilogram of body weight therefore, the picture is complicated, for the large animal must be compared with two much smaller animals, and there was an appreciable difference in the lengths of the fasts, the effect of which is certainly, with the small

python, to lower the metabolism. Although, therefore, at first sight the four curves in figure 48 seem to agree fairly well with each other, if due weight is given to the definitely established differences in the two curves for the small Indian python, the large python may not be directly compared with the small Indian python or the 1931 python, because not under the same condition as regards length of fasting. Notwithstanding these differences in the levels of the curves, the average trend of the four curves has been indicated by the heavy black line, and this average curve will be used in a subsequent comparison of all the different species of cold-blooded animals (see pages 243 and 426). It is realized that this average curve can not be used to predict the metabolism of the python at any given temperature, but that it suggests only the general trend of the python's metabolism.

#### HEAT PRODUCTION PER SQUARE METER OF SURFACE AREA

Rubner has emphasized that when one is comparing the metabolism of animals of different weights, a correction must be made for these differences in weight by comparing the metabolism per unit of surface area. This correction he recognized even in the case of the cold-blooded animals of the same species.<sup>1</sup> In this study with the small Indian python, differences in body weight actually occurred, for the weights ranged from a minimum of 5.82 kg. to a maximum of 7.43 kg. If the general thesis is to be accepted that the best comparison is made upon the basis of surface area, the results for the three pythons should be calculated on the basis of the standard heat production per square meter of body surface, in the attempt to wipe out the differences in body weight existing with these animals from time to time in our study. These calculations have been made for the small Indian python and recorded in table 52 (p. 197). The body surface was computed in accordance with the method outlined in a previous section (pages 144 to 148), using 12.5 for the factor K in the formula  $S = K \times w^{2/3}$ . Obviously one wonders why, if the surface area of the small Indian python was actually measured, it was not used throughout the entire series of calculations. It so happens that on the dates of the metabolism experiments the small python did not weigh exactly the same as it did on the day the surface area was measured. On the other hand, as was pointed out in the surface-area discussion, it is difficult to conceive how the body surface of a snake could alter even with changes in body weight, for when a snake is greatly emaciated as a result of prolonged fasting, the skin hangs in great folds and there is apparently no decrease in the skin area. Emaciated snakes, as a rule, do not contract the skin, in spite of the great distensibility of the skin following eating (see page 142). Rubner has rightly emphasized the importance in such comparison of the animals being in a good nutritive state. However, it seemed best to make the surface-area calculations on the accepted basis of employing a constant to be applied to the two-thirds power of the body weight.

The values for the standard heat production of the small Indian python per square meter of body surface have been plotted in figure 49, referred

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 229.

to environmental temperature. On this chart against each plotted point has been indicated the number of days that the python had been fasting. Here again there are two curves comparable to those in the chart in which the comparison was made on the body-weight basis, that is, one curve for the longer fast and another curve for the shorter fasts. These two

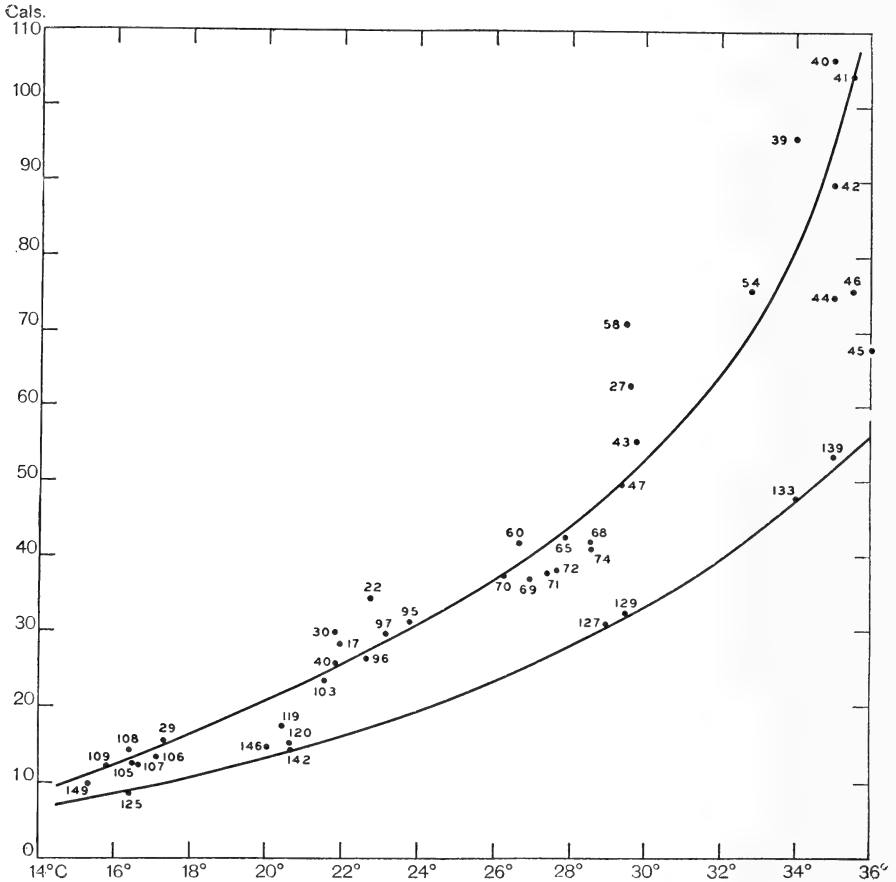


FIG. 49—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—SMALL INDIAN PYTHON.

Value against each plotted point indicates number of days snake had been fasting. Lower curve represents trend of metabolism in longer fasts and upper curve trend in shorter fasts.

curves have been sketched on this chart in much the same manner as were the curves for the weight comparison (fig. 45, p. 199). The general picture of the two curves is essentially that shown in the comparison on the body-weight basis. In other words, the actual change in the computed surface area of this python was so small during the period of observations with it (13 per cent) that the general trends of the two curves on the body-surface

basis are not materially different from those on the weight basis.<sup>1</sup> As will be seen from table 52 (p. 197), at or near the body temperature of man, that is, at 38° C., the indirectly measured heat production of this python when fasting 22 days rose to 129 calories per square meter of body surface per 24 hours. This heat production is only about one-seventh that of the adult human or one-eighth of the commonly accepted value for all warm-blooded animals of 1000 calories per square meter of body surface.<sup>2</sup> There is a great scatter in the plotted points in figure 49 and these curves at best represent only general trends.

For the large python the standard heat production has likewise been computed per square meter of surface area (table 54, p. 205) and the results have been plotted with reference to the environmental temperature in figure 50. The body surface was calculated to be 1.44 square meters, based on the factor of 14.4 as derived from measurements of its length and various girths (p. 146). Here the body weight was taken as the same throughout the entire series of measurements, so one would expect and does find a curve identical in form with that for the heat production per kilogram of body weight. No special discussion of this chart is necessary other than to point out that at the highest temperature at which the large python was studied, 29.5° C., the average standard heat production was 73 calories per square meter of body surface per 24 hours. If the curve were projected to 38° C., the heat production as indicated by the curve would in all probability be materially higher than that noted with the small Indian python, that is, nearer 200 than 129 calories.

For the 1931 python the body surface has again been computed from the formula  $S=K \times w^{2/3}$ , in which K has been considered to be 12.5, the average value found for all the snakes that were measured. At the time the calculations of the heat production per unit of surface area were first made for this python, the body measurements of the animal had not been obtained and the skin area had not been directly measured. For the reasons pointed out in our discussion of the measurement of the skin area (p. 142) it is believed that the measurements of the skin area, either by means of planimetering the photograph or by counting the square inches enclosed in the traced outline of the skin on the cross-section paper, are erroneous and that the body-surface constant of 13.0 calculated from the measured length and girths of the 1931 python is in all probability correct. The difference between 13.0 and 12.5 is so small, however, that it is believed the general average of 12.5 is fully as justifiable for the purposes of this comparison as the actually determined constant of 13.0. Therefore 12.5 has been used for the 1931 python as well as for all the other snakes except the

<sup>1</sup> Undoubtedly as both Murlin (Science, 1921, **54**, p. 196) and Rubner (Biochem. Zeitschr., 1924, **148**, p. 288) have correctly emphasized, F. G. Benedict has not at times properly sensed the important point that the surface-area calculation can affect the situation only when there are *considerable* differences in body weights.

<sup>2</sup> Rubner (Sitzungsb. d. preuss. Akad. d. Wissensch., Phys.-Math. Kl., 1931, **17**, p. 313) has recently emphasized that the value of 1000 calories pertains to the metabolism of mammals at 16° C. He considers that if the heat production of mammals were to be measured at 30°, that is, at the minimum level or at the level of thermic neutrality, the value would be nearer 615 calories per square meter of body surface per 24 hours.

large python. The results for the standard heat production of the 1931 python per square meter of body surface referred to environmental temperature are shown in figure 51. Here again, as in the case of figure 47, the values plotted with reference to the rectal temperature have been indicated by crosses, those plotted with reference to the environmental temperature by dots, and those obtained up to and including January 24, *i.e.*,

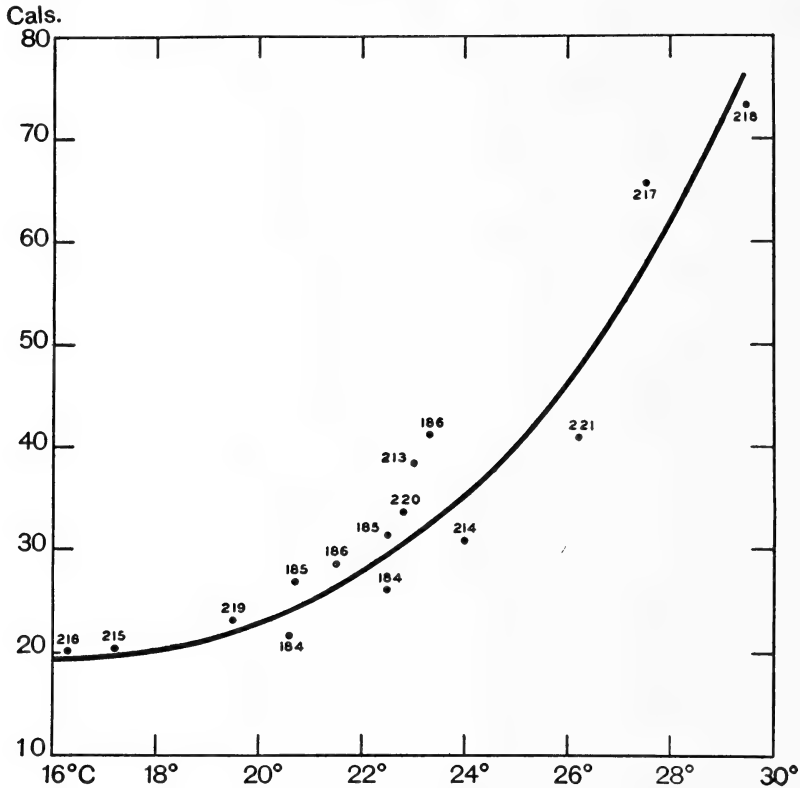


FIG. 50—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—LARGE PYTHON.

Value against each plotted point indicates number of days snake had been fasting.

before the digestion period, have been enclosed in circles. Theoretically it could be argued that with one and the same animal the metabolism results, whether computed per unit of weight or of surface area, would show the same general picture when plotted with reference to the environmental temperature. But since the 1931 python weighed on the average 5.4 kg. prior to the ingestion of food on January 24 and 6.3 kg. after the food had been digested, it might be assumed that the calculation per unit of surface area would equalize more closely this difference in size. The curve drawn through the plotted points in figure 51 shows the same general trend as did the curve for the heat production per kilogram of body weight, with much the same scatter of points above and below the line as before. It is clear,

however, that with any one given animal the scatter of points is far less than would be the case if the chart contained the plotted data for a large number of different animals. (See figures 54 and 60, pages 224 and 229.) The average heat production of the 1931 python is about 10 calories per square meter of body surface per 24 hours at 18° and rises to a maximum of 101 calories at 38° or 39°.

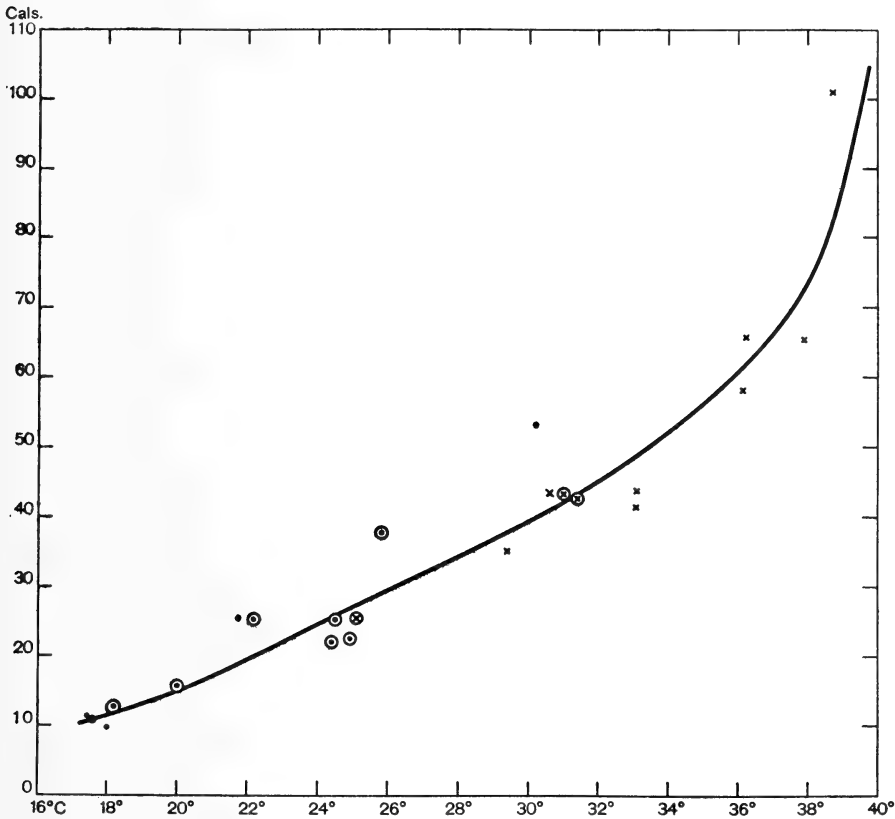


FIG. 51—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL OR BODY TEMPERATURE—1931 PYTHON.

Dots and crosses enclosed in circles indicate values obtained before digestion period; those not enclosed in circles values after digestion period. Dots represent values plotted with reference to environmental temperature and the crosses values plotted with reference to rectal temperature.

A direct comparison of the metabolism of the three pythons referred to body surface is best made by means of a chart on which the curves for these snakes are drawn, unobscured by the individual points (fig. 52). This comparison shows that whereas on the body-weight basis the curve for the large python lies for the greater part of its length between the two curves for the small Indian python, on the body-surface basis it lies throughout its entire length materially above even the higher of the two curves for the small Indian python. Precisely the same argument presented before, how-

ever, with regard to the state of fasting holds true here. The influence of prolonged fasting in lowering the metabolism of the small Indian python has been demonstrated. In all probability the longer fast of the large python had likewise reduced its metabolism measurably so that if a correction could be made for the length of fasting, the curve for the large python in figure 52 would lie materially higher than it is at present. If one compares the curve for the large python which fasted on the average about 200 days, with the lower curve for the small Indian python when this snake

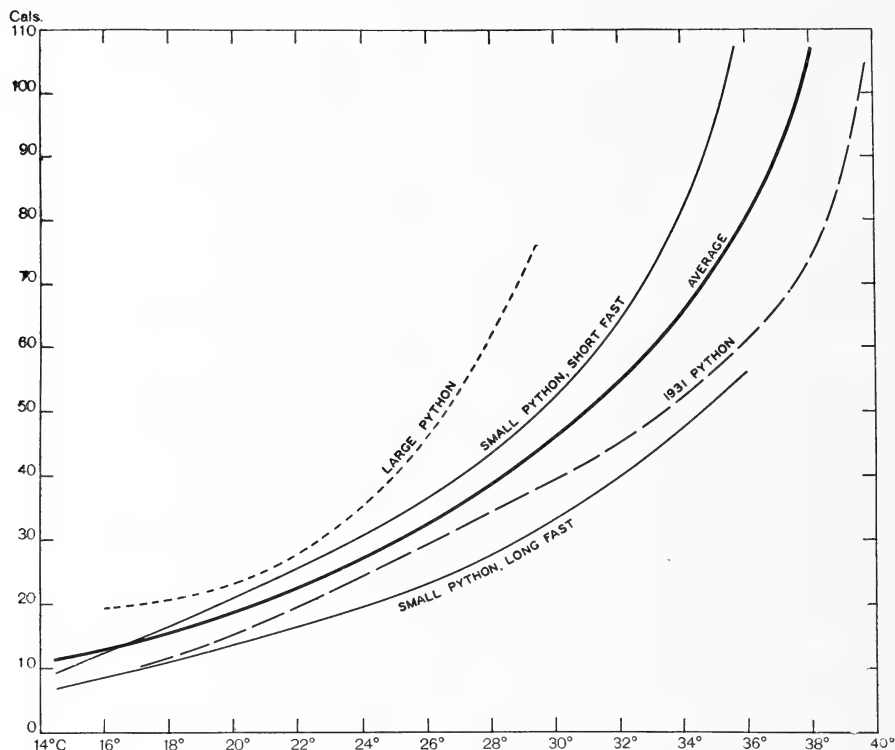


FIG. 52—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO TEMPERATURE—ALL PYTHONS.

had fasted on the average 135 days, one can see that the metabolism is measurably higher with the larger animal. Thus, at 18° the metabolism per square meter of body surface is essentially twice as great with the large python as with the small Indian python. At 28° the heat production of the small python is about 27 calories per square meter of body surface and that of the large python is 62 calories or more than 100 per cent greater. Hence it is clear that on the basis of the heat production per square meter of surface area the large python gives values on the whole nearly 100 per cent higher than those for the small python. On the other hand, if the curve for the heat production of the large python per kilogram of body weight in figure 48 is compared with that for the small Indian python during prolonged fasting, it is found that the curve for the large

python gives values always higher than those indicated by the curve for the small python, but not so much higher as on the body-surface basis. Thus, at 18° the standard heat production of the large python per kilogram of body weight is about 40 per cent above that of the small Indian python, and at 28° it is about 45 per cent. It would appear, therefore, that in general the heat production per kilogram of body weight is less variable, so far as these two pythons are concerned, than is the heat production per square meter of body surface. But the variability on either basis of comparison is so great that one can hardly call the heat production of these two cold-blooded pythons uniform.

The curve for the standard heat production per square meter of body surface for the 1931 python has likewise been included in figure 52 and, as in the case of the metabolism per unit of weight, lies about midway between the two curves for the small Indian python. As before, a heavy black line has been drawn to indicate the average trend of the different curves, and this average curve will be used subsequently in the comparison of snakes of different species and of cold-blooded animals in general (see pages 245 and 428). The comparison of the standard metabolism of these three pythons is complicated by the fact that the 5-meter snake was some 25 kg. heavier than the other two snakes. Likewise the large python was not precisely of the same species as the other two animals (see page 8), although of a closely allied species. It is unfortunate that more pythons could not have been measured, particularly in a relatively uniform state of nutrition, and especially with regard to the time after eating. It is difficult to judge the state of nutrition of these animals. They withstand fasting for a long time without giving any ocular evidence of appreciable emaciation, and yet a relatively short fast has seemingly a pronounced effect upon the metabolism, as is seen with the small Indian python. The well-known fact that snakes fold in upon themselves so much that the actual area exposed to the temperature of the environment may be different with two different snakes, even of the same size, further complicates the situation. This coiling of the serpent possibly is a factor entering into these comparisons and might, in the minds of some writers, account to some extent for the large variability noted in the individual points on the charts.

A general comparison of figures 48 and 52 is justifiable because, although the ordinates have different values, percentagewise the increase in the value of the ordinates is the same. These two charts show that the agreement between the different pythons is much closer when the heat production is expressed per kilogram of body weight than when it is expressed per square meter of body surface. This, in addition to the fact that comparison of the largest python with the smallest python indicates a pronounced difference in the two methods of expression in favor of the body weight basis, leaves no doubt that with these pythons the heat production per unit of weight was much more uniform than that per unit of surface area, in spite of the differences in body weight. A more detailed analysis of these two bases of comparison will be made later, when snakes as a whole and particularly cold-blooded animals as a whole are considered (see pages 242 and 426).



COMPARISON OF HEAT PRODUCTION OF BOAS  
HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT

Fortunately among the boas more than three snakes were studied, and although none was as large as the 5-meter python, nevertheless the percentage difference in the body weights of the boas was nearly as great as that noted with the pythons. Hence a comparison of the standard metabolism of the 14 boas studied is in order. Boa B was a Cuban boa; all the others were South American boas. In contrast with the nervous, irritable pythons, they were for the most part quiet and unperturbed during handling. Marked differences were found in the nature of the general curves for boas A, B and C, indicating the trend of the standard heat production per kilogram of body weight (see figs. 41, 42 and 43, pages 159, 160 and 161). The data for boa A are particularly striking, for the three observations at 35° and above show a metabolism on the whole no higher than that at about 30° C. The three measurements at the higher temperature were made with considerable intervals between them, one on November 4, 1915, one on February 10-11, 1916, and one on February 15-16, 1916. In the first case the duration of the period was 4 hours, in the second and third cases 17 hours each. Therefore the results are based upon well-founded experimental periods. The plateau in metabolism seemingly established with boa A was not observed with boa B, but with boa C there was a tendency for the metabolism to seek somewhat of a level between 29° and 33° C. With such irregularities in the curves showing the general trends with the individual boas, we are prepared to note pronounced differences when the data for all 14 boas are compared.

In figure 53 the general curves for boas A, B and C are presented, and since there are not sufficient data for boas D to N to justify a smoothed curve for each one, we have plotted the individual values for the standard heat production per kilogram of body weight per 24 hours referred to environmental temperature. The boa's identity has been indicated against each plotted point and for boa D's prolonged fast the number of days fasting. The curve for boa C lies below the curve for boa A except at about 16° C., and the curve for boa A lies throughout its entire length below that for boa B. The Cuban boa, B, therefore seems to have a higher metabolism throughout the entire range of temperatures studied than either boa A or boa C. It so happens that although the observations on boa A extended over a period of four months, on boa B but one month, and on boa C two months, there were no great changes in the body weights and all three snakes had nearly the same weight, boas B and C weighing about 12.5 kg. and boa A about 10 kg. The low metabolism of boa C between 20° and 24° C. is well established by a number of observations, as is seen by reference to figure 43. At 16° and 17° both boas A and C have nearly the same metabolism. Boa D shows the greatest individual irregularity of any of the boas. Indeed, so great is the scatter of the points for this snake that we did not feel justified in laying on a curve in figure 44 (p. 168) and therefore have not drawn a curve for it in figure 53.

From our observations with the small python, the length of fasting seemed to play a considerable rôle in that the metabolism was lower with

prolonged fasting. On the other hand, the large python had fasted somewhat longer than the small python and yet had a higher metabolism, both per kilogram of body weight and per square meter of body surface. In originally preparing figure 53 for the boas, the length of time that the boa had been fasting and the body weight of the snake were written against each plotted point. This information has been omitted from the chart as finally published, since it obscured the picture, but it was helpful in the detailed analysis of the data, especially in studying the effect of fasting. With but two exceptions, the fasts were not unusually long. With boa D, however, two observations were made when it had been fasting 1 year and 58 days and 1 year and 141 days, respectively. These observations are

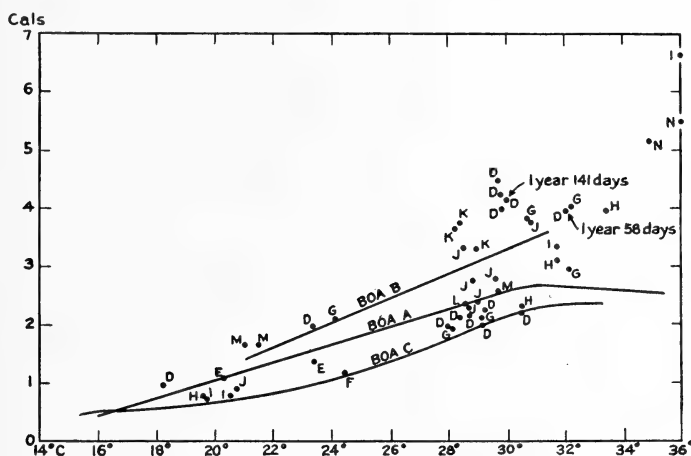


FIG. 53—COMPARISON OF STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS, WITH REFERENCE TO ENVIRONMENTAL TEMPERATURE, OF BOAS A TO N, INCLUSIVE.

Letters against plotted points indicate individuality of boas. Points marked "1 yr. 58 days" and "1 yr. 141 days" show the level of metabolism of boa D after prolonged fasting.

indicated in figure 53. No correlation is found between these points and the length of fasting to aid in clarifying the seemingly great distribution of the plotted points for the 14 boas, for in spite of this long fasting the metabolism of boa D per kilogram of body weight is much higher than that of most of the other snakes measured at the same temperature.

With a compound chart like that in figure 53, made up of curves for boas A, B and C and a large number of points for the other boas, it would obviously be inconsistent to lay on any curve showing the general trend of the metabolism of all the boas, for it would be impossible to give due weight to the large number of points entering into the make-up of the curves for boas A, B and C. A second chart has therefore been prepared (fig. 54) in which the data for all 14 boas have been plotted, one point for each separate experiment, and thus the individuality of each snake has been completely lost. The average trend of the standard metabolism of the 14 boas is represented by the heavy black curve sketched through the plotted

points. On this chart, in which the standard 24-hour heat production per kilogram of body weight has been referred to environmental temperature, one sees more clearly than ever the wide scatter of points, especially beyond  $28^{\circ}\text{C}$ . This confirms the observations drawn from the previous charts that the standard metabolism of the cold-blooded snake at the higher temperatures is more labile than at the lower temperatures. It is thus seen that with these boas as a group there is nothing approximating uniformity in metabolism with increasing temperature, as is shown in the regular curve presented by Krogh for the standard metabolism of cold-blooded animals at different temperatures.<sup>1</sup>

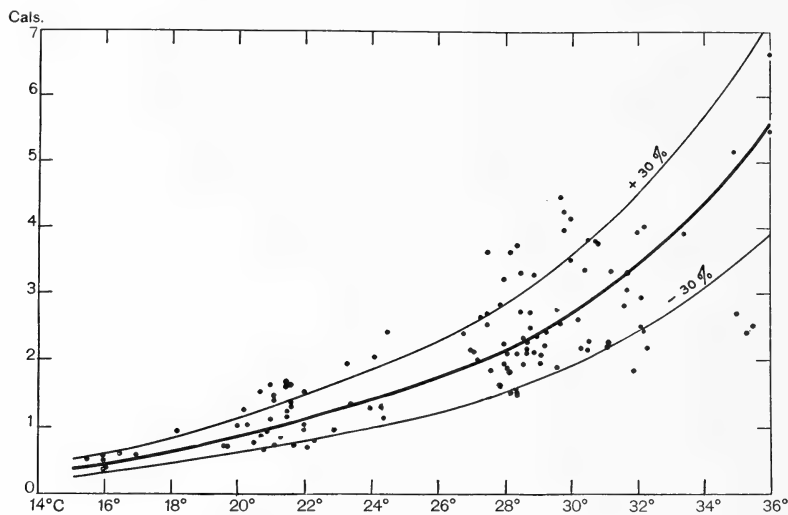


FIG. 54—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—ALL BOAS.

Heavy black curve in center indicates *average trend* of metabolism of all boas with increasing environmental temperature. Lighter curves above and below heavy black curve indicate trend of metabolism with increasing temperature 30 per cent above and below average trend.

One of the main values of the average curve drawn in figure 54 is for comparison with the curves for the pythons and the other cold-blooded animals. The scatter of the plotted points on this chart is so wide that it is futile to attempt to compute the total metabolism of any snake of a given body weight from a chart such as this. To give some indication of the wideness of the scatter, we have sketched in figure 54 two curves representing the average trend of the metabolism 30 per cent above and 30 per cent below the heavy black curve typifying the general course of the metabolism of all the boas. Twenty or more of the plotted points lie outside even these two limits. Possibly the larger number of boas studied accounts for the fact that the picture is altogether different from that shown by the pythons. With the pythons, in spite of their difference in size (32 and 5

<sup>1</sup>Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, p. 96; *ibid.*, Internat. Zeitschr. f. physik.-chem. Biol., 1914, 1, p. 504.

to 7 kg.), there was a reasonably close relationship between the temperature of the environment and the heat production per kilogram of body weight, but with these boas there is no close correlation between these two factors. The general curve drawn in figure 54, the middle curve, may be of value, however, in suggesting the general trend of the metabolism of boas and may possibly be of service in comparing the standard heat production per unit of weight of boas in general with that of the pythons and the other snakes, as well as the lizards, alligators and tortoises.

#### HEAT PRODUCTION PER SQUARE METER OF SURFACE AREA

Reverting again to the time-honored method of comparing the metabolism of animals of different sizes with reference to their surface area and basing our calculations of the surface area upon our own extensive series of measurements of length and girth, we have computed the standard heat production per square meter of surface area for boas A to N. These calculations have already been presented in tabular form in a preceding chapter

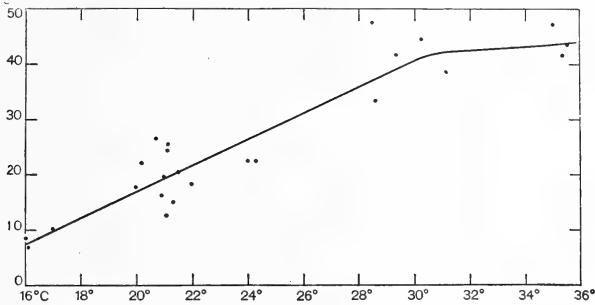


FIG. 55—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—BOA A.

(pages 157 to 182) and the results for boas A, B, C and D, which were the most extensively studied, have likewise been plotted with reference to the environmental temperature, for each boa separately. In figure 55 an attempt has been made to lay on a curve showing the general trend of the standard heat production of boa A per square meter of body surface at increasing environmental temperatures. One of the most striking features of this curve is the apparent constancy in metabolism between 30° and 36° C., a point already emphasized in the consideration of the metabolism of this boa per kilogram of body weight. The maximum heat production noted in the different experiments with boa A was 47.7 calories per square meter of body surface at 28.5° and the minimum was 7.0 calories at 16.1° C.

With the Cuban boa, B, a more regular trend in the metabolism is shown by the curve in figure 56. It will be recalled that in figure 42 (p. 160), in which the heat production per kilogram of body weight of this boa was referred to environmental temperature, the general trend was better shown by a straight line. Here the line is curved. The maximum heat production per square meter of body surface was 72.1 calories and the minimum 24.9 calories at correspondingly high and low temperatures.

The large number of measurements obtained with boa C have been computed with reference to the body surface and plotted in figure 57. The maximum value is 52.3 calories per square meter of body surface at 31.6° and the minimum is 7.4 calories at 16° C. The curve representing the

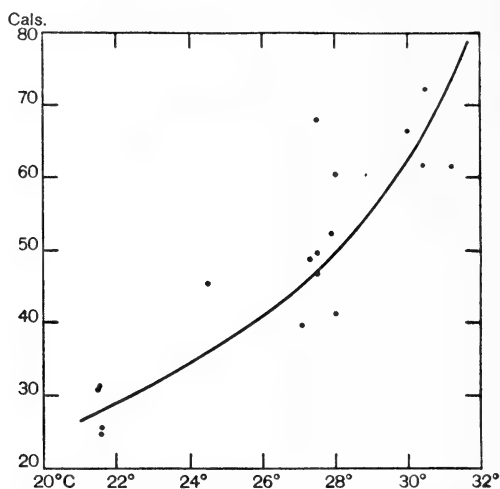


FIG. 56—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—BOA B.

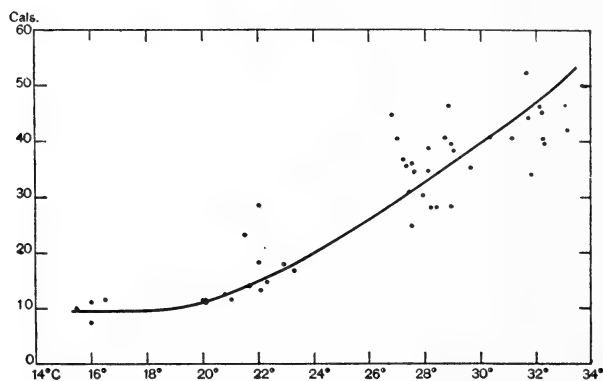


FIG. 57—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—BOA C.

general trend of the standard metabolism fits the plot fairly well. There is a suggestion of constancy in the metabolism between 16° and 20°. The scatter of the plotted points becomes wider as the temperature goes up, bearing out again our belief that at the higher temperatures the standard metabolism of these cold-blooded animals is extremely variable.

With boa D the situation is represented in figure 58. Here the distribution of the plotted points is so great (duplicating the picture in figure

44 dealing with the heat production per kilogram of body weight) that we have not felt justified in drawing any curve through these points. Particularly noticeable is the fact that at or about  $30^{\circ}$  the metabolism of this snake ranges from 84.3 calories to about half of that or 40.9 calories, and the fact that after over one year of fasting the metabolism at  $30^{\circ}$  may be as high as 63 calories per square meter of body surface.

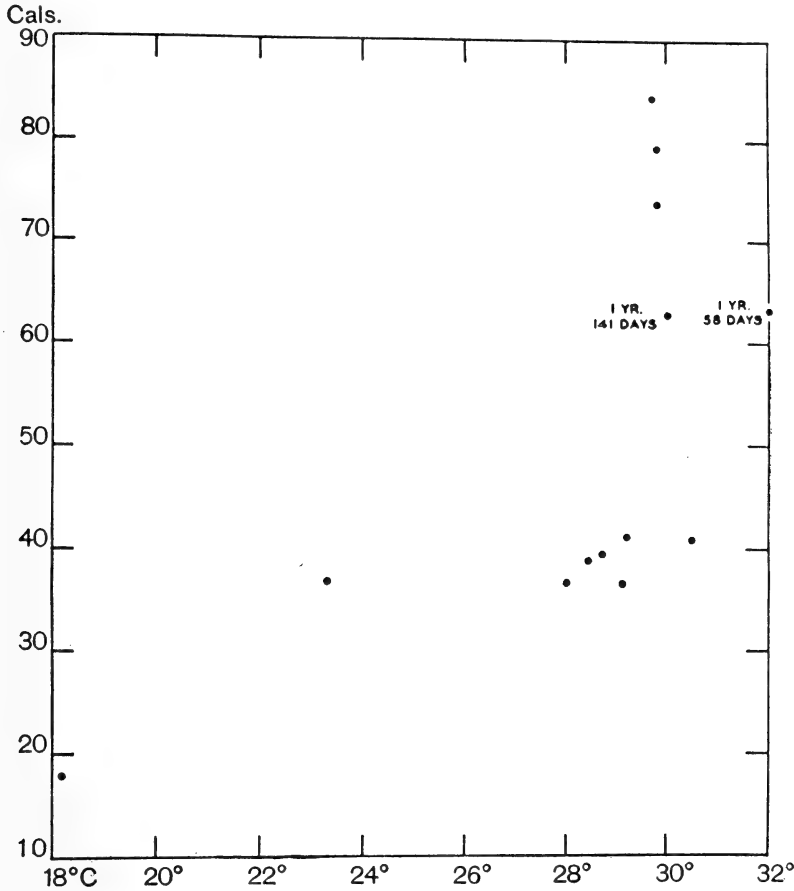


FIG. 58—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—Boa D.

The most definite method for comparing all these boas with respect to their body surface is that adopted in the comparison of the metabolism per kilogram of body weight in figure 53. We have accordingly plotted in figure 59 the standard 24-hour heat production per square meter of body surface referred to environmental temperature. For boas A, B and C, we have used the curves drawn from their respective charts, figures 55, 56 and 57. The other boas, including boa D with its aberrant figures, are indicated by points, each point representing the average metabolism on a given experimental day. The identity of the boa has been written against each

point. Our attention is first called to the comparison of the three curves for boas A, B and C, which are here brought together. On the basis of the heat production per square meter of surface area as well as on the body-weight basis, the Cuban boa, B, has much the highest metabolism of the three snakes. The curve for boa C, which on the basis of the heat production per kilogram of body weight lies throughout practically its entire length below that for boa A, now on the basis of surface area rises

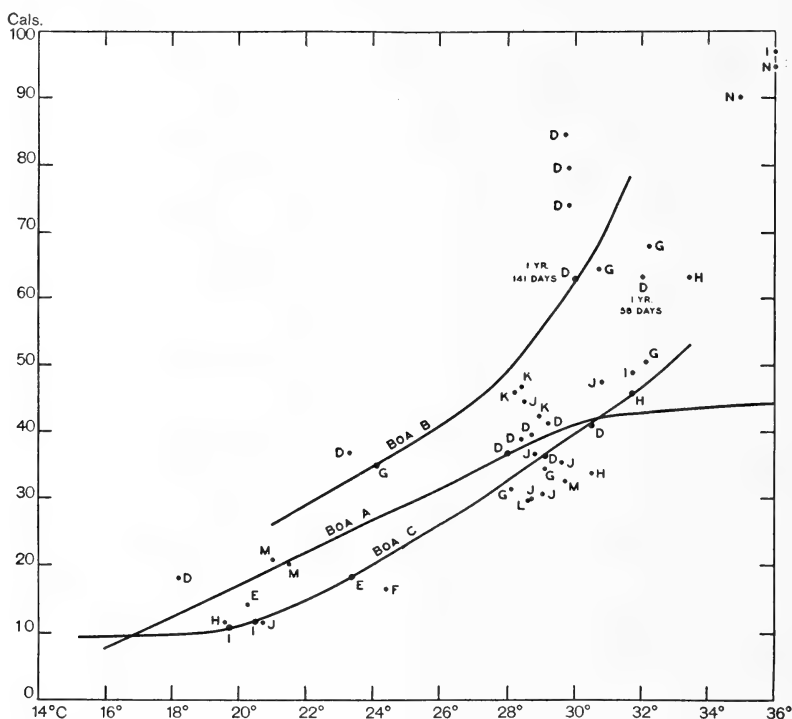


FIG. 59—COMPARISON OF STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE, WITH REFERENCE TO ENVIRONMENTAL TEMPERATURE, OF BOAS A TO N, INCLUSIVE.

Letters against plotted points indicate individuality of boas. Points marked "1 yr. 58 days" and "1 yr. 141 days" show level of metabolism of boa D after prolonged fasting.

above the curve for boa A at 30.6° C. The propriety of drawing a curve through the plotted data in figure 53 representing the heat production per kilogram of body weight for all the boas was questioned. It is still more debatable whether one is justified in attempting to sketch a general, representative curve in figure 59, where the values are so widely scattered. This has not been done.

In order to compare directly the heat production of these 14 boas per square meter of body surface referred to environmental temperature, we have plotted in figure 60 all the values for all the boas, but have not shown the individuality of any of the snakes. The difficulty of laying on a general curve is immediately recognized, but we have ventured to do so, as

shown by the heavy, black line. Lighter lines, representing the trend of the metabolism 30 per cent above and below this general average curve are likewise placed on the chart. A rough index of whether the metabolism per unit of surface area is any more uniform than that per unit of weight may be obtained by counting those points lying more than 30 per cent above or below the average curve in figure 54 (p. 224) and in figure 60. There are essentially the same number of points outside these limits on

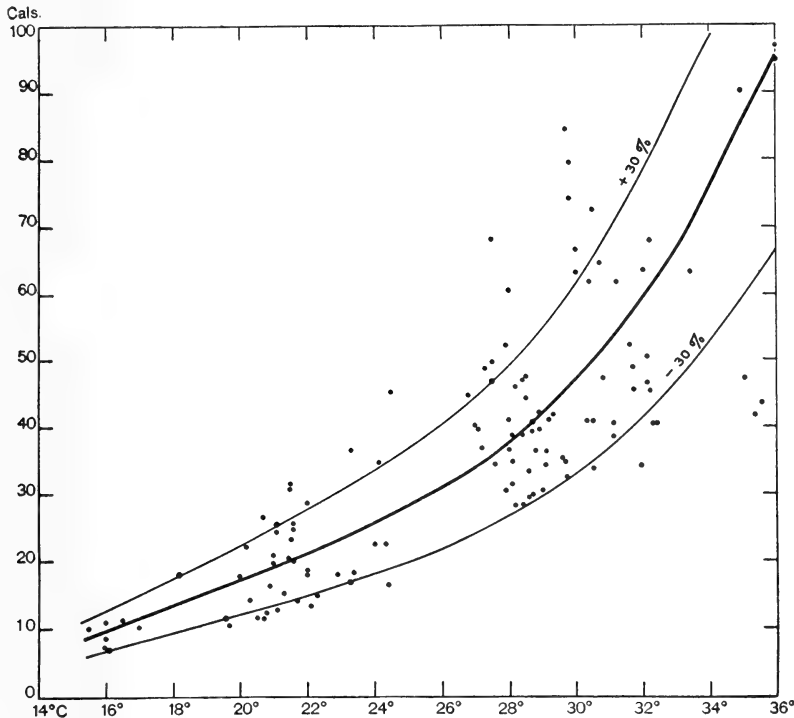


FIG. 60—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—ALL BOAS.

Heavy black curve in center indicates *average trend* of metabolism of all boas with increasing environmental temperature. Lighter curves above and below heavy black curve indicate trend of metabolism with increasing temperature 30 per cent above and below average trend.

both charts. This is crude evidence that the heat production per square meter of body surface is certainly no more uniform than the heat production per kilogram of body weight. In this respect the boas differ from the pythons, for with the pythons it is clear that the metabolism per unit of weight is less irregular than that per unit of surface area.

In any consideration of figure 60, however, it is important to note that, according to the surface-area law, any greater uniformity in the metabolism on the basis of surface area is to be expected only when there are large differences in body weight. In the case of the two pythons there



was a large difference in their weights. In the case of the boas (as will be seen from table 57), 103 of the 134 observations plotted in figure 60 were obtained upon boas weighing from about 10 to 13 kg. Five of the 14 boas weighed as low as between 3 and 5 kg., but the total number of points on the chart for these boas is but 16. Consequently the data presented in figure 60 are for the most part for boas whose body weights were essentially uniform, and it is therefore to be expected that the distribution of the points on the basis of surface area is not greatly different from that on the basis of body weight. The individual values for the different snakes vary so greatly, as is seen from figures 55, 56 and 57 for boas A, B and C, that it would be difficult to compare, for example, boa B at a weight of 12.90 kg. with boa M at a weight of 3.4 kg. Because of the number and

TABLE 57—*Comparison of maximum and minimum weights and number of observations on each boa*

Boa	Body weight		Number of observations	Boa	Body weight		Number of observations
	Maximum	Minimum			Maximum	Minimum	
	<i>kg.</i>	<i>kg.</i>			<i>kg.</i>	<i>kg.</i>	
A.....	10.23	9.53	24	E.....	4.86	4.64	2
B.....	12.90	11.82	17	F.....	5.73	.....	1
C.....	12.45	11.82	47	G.....	9.37	8.32	6
D.....	12.96	6.69	13	H.....	7.99	6.49	4
N.....	10.15	10.08	2	I.....	6.25	6.02	4
				J.....	4.59	3.64	7
				K.....	3.89	3.79	3
				L.....	4.05	.....	1
				M.....	4.06	3.41	3
Total.	.....	.....	103	Total.	.....	.....	31

wide scatter of points it would be too confusing to put on figures 60 and 54 the actual weights of the different boas. Direct comparison, by means of these charts, of snakes of large and small weights, either on the basis of the heat production per kilogram of body weight or the heat production per square meter of body surface, is ruled out. Such a comparison, however, is not without importance, for in accordance with the belief that the surface-area law obtains more particularly when large differences in mass are to be equalized, we would expect to find a greater uniformity in the heat production per square meter of body surface than in that per unit of weight, when comparing two snakes of widely different body weights.

INFLUENCE OF SIZE AND COMPARISON OF METABOLISM EXPRESSED PER UNIT OF WEIGHT AND PER UNIT OF SURFACE AREA

To study more specifically the influence of size *per se* upon the standard metabolism, we have recorded in table 58 the 24-hour heat production both per kilogram of body weight and per square meter of body surface of those boas measured at about 21° and 29° C. These two temperatures were chosen as being below the high temperatures at which the pronounced

irregularities in the metabolism of boas A and C were noted. The values in table 58 for boas A, B and C, *i.e.*, heavy boas, are based upon their respective smoothed curves in figures 53 and 59. The values for the other boas, E, I, J, K, L and M, *i.e.*, boas of small weight, are derived not from curves but from actual observations with them at these temperatures. Comparing the data at 21° C. for boas A, B and C, we find that the range in the metabolism per unit of surface area is about the same as that per unit of weight. Thus, the calories per kilogram of body weight range from

TABLE 58—*Comparison of standard metabolism at 21° and 29°, of boas weighing 10 to 12 kg. and boas weighing 3 to 6 kg.*

Environ- mental temperature and boa	Body weight	Heat produced per 24 hours		Per cent of average for boas A, B and C	
		Per kg.	Per sq.m.	Per kg.	Per sq.m.
21° C.:	<i>kg.</i>	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>
A.....	10	1.19	19.0	.....	.....
B.....	12	1.50	27.5	.....	.....
C.....	12	.72	12.3	.....	.....
Avg....	10 to 12	1.14	19.6	100	100
E.....	5	1.05	14.2	92	72
I.....	6	.79	11.6	69	59
J.....	4	.89	11.4	78	58
M.....	3	1.65	20.1	145	103
Avg....	3 to 6	1.10	14.3	96	73
29° C.:					
A.....	10	2.41	39.0	.....	.....
B.....	12	3.10	55.5	.....	.....
C.....	12	1.97	36.2	.....	.....
Avg....	10 to 12	2.49	43.6	100	100
J.....	4	2.78	36.9	112	85
K.....	4	3.69	46.4	148	106
L.....	4	2.34	29.6	94	68
M.....	4	2.57	32.5	103	75
Avg....	4	2.85	36.4	114	84

0.72 with boa C to 1.50 or 205 per cent as much with boa B. Per unit of surface area the range is from 12.3 to 27.5 calories, or 224 per cent. The average values for boas A, B and C at 21° are 1.14 and 19.6 calories per unit of weight and per unit of surface area, respectively. The four smaller boas, E, I, J and M show considerable deviations from these averages, the metabolism per kilogram of body weight ranging from 0.79 calorie with boa I to 1.65 calories with boa M and the metabolism per square meter of body surface from 11.4 calories with boa J to 20.1 calories with boa M. The values for boas E, I and J at 21° C. do not differ greatly from each other, however, on either basis. They agree fairly well with the values

for boa C on both bases, but are much lower than the results for boas A and B. With boa M, on the other hand, the values are greater than with boas E, I and J, and more closely approximate the results for boas A and B. From this general inspection of the data at 21° C., one certainly can not say that there is less variability in the heat production per unit of surface area than in that per unit of weight. At the higher temperature of 29° C. boas A, B and C have an average heat production of 2.49 and 43.6 calories, respectively. The values for the smaller boas range from 2.34 calories with boa L to 3.69 calories with boa K per kilogram of body weight and from 29.6 calories with boa L to 46.4 calories with boa K per square meter of body surface. Boa K, one of the smallest boas, is characterized by having a high metabolism.

The simplest method of comparing these values, with special reference to the uniformity of results, is to express them on the percentage basis. We have arbitrarily considered the average values for boas A, B and C as representing 100 per cent and for each of the smaller boas have calculated what percentage their metabolism is of the average metabolism of the larger boas. At 21° C. the percentages range from 69 with boa I to 145 with boa M on the weight basis, a wide range. On the body-surface basis the range is from 58 to 103 per cent. On the average the heat production per kilogram of body weight with the four small boas, each weighing not far from 4 kg., is 96 per cent of the average for the three large boas weighing 10 to 12 kg. On the body-surface basis the four small boas have a metabolism only 73 per cent of that of the large boas. This comparison indicates that the heat production per kilogram of body weight is the more uniform. The values for boa M are the most aberrant. Even if these are left out of the comparison, the average percentages for boas E, I and J are 80 on the weight basis compared with 63 on the area basis.

At the higher temperature of 29° C. the situation is somewhat different. Taking the average values for boas A, B and C again as equal to 100 per cent, we find that on the body-weight basis three of the small boas run above this. Boa L is the only exception with a metabolism 94 per cent of the average heat production per kilogram of body weight. Boa K, on the contrary, has a metabolism equivalent to 148 per cent of the average. On the surface-area basis the range is from 68 per cent with boa L to 106 per cent with boa K, that is, for the most part below the average for boas A, B and C. The average for the four small boas on the weight basis is 114 per cent and on the area basis 84 per cent, that is, there is an excess of 14 per cent on the weight basis and a deficit of 16 per cent on the area basis. There is thus a slight advantage of 2 per cent in favor of the body-weight expression. The general picture from table 58 is that even with these extreme differences in body weight of from 12 to 3 or 4 kg., the results do not show a pronounced advantage in favor of the surface-area comparison. At 21° C. there is an advantage of 23 per cent in favor of the comparison per unit of weight and at 29° C. an advantage of 2 per cent. Hence the specific illustrations in table 58 bring out more sharply what was inferred in a general way from the rough comparisons in figures 54 and 60, in which the detailed data for all the boas are plotted at one

time and in which a large proportion of the points are for boas weighing approximately 10 to 12 kg. The question proposed was as to whether there is any advantage in the use of the surface-area comparison. With the wide differences in body weight illustrated in table 58 there is a slight advantage in favor of the body-weight expression at 29° C., and a greater advantage at 21° C. The only conclusion therefore is that reference of the metabolism to the unit of surface area is of no material value in the comparison of these boas of widely different weights.

Before leaving the comparison of the heat production per unit of surface area and per unit of body weight, a still further consideration seems justifiable. The heat production per kilogram of body weight referred to the body weight of two selected groups of boas, the first group averaging about 4 kg. and the second about 12 kg., has been plotted in figure 61, using only measurements made on the animals between 27° and 29°, thus essentially ruling out the effect of temperature. With the boas averaging

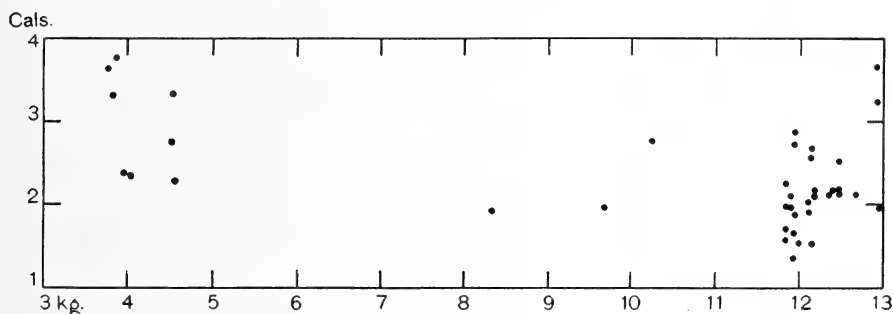


FIG. 61.—COMPARISON OF STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO BODY WEIGHT—BOAS WEIGHING ABOUT 4 AND 12 KG.

Environmental temperature in all these experiments was between 27° and 29° C.

4 kg. the heat production is about 3 calories per kilogram of body weight per 24 hours. With the boas averaging 12 kg., although the data scatter considerably, the average is not far from 2.15 calories. Thus the metabolism of the smaller boas is almost 50 per cent higher than that of the larger boas at the same temperature. Plotting the data for the same boas on the basis of the heat production per square meter of body surface in figure 62, we see that the average metabolism of the 4-kg. group (there is a rather considerable scatter of the plotted points, to be sure) is 39 calories and of the 12-kg. group (likewise showing a wide scatter) not far from 40 calories. Certainly the metabolism of these two groups of boas of greatly different weights is much more uniform when expressed as the heat production per square meter of body surface.

A still further comparison can be made by inspection of figures 54 and 60, in which the data for all the boas have been plotted. Thus, in figure 54, if we consider only boas measured between 27° and 29°, we find that on the body-weight basis there are two points below the -30 per cent line and nine points above the +30 per cent line. Within the same temperature range in figure 60—on the body-surface basis—there are no points

below the  $-30$  per cent line and but five points above the  $+30$  per cent line. This comparison shows that there is a distinct tendency for a closer agreement of the extreme values when computed per unit of surface area. Although the picture in general, therefore, might be taken as indicating no material difference between the two methods of expression, more detailed analysis of figures 54 and 60 leads to the conviction that the metabolism of the boas shows a somewhat closer agreement per square meter of body surface than per kilogram of body weight. To be sure, the difference between 4 and 12 kg. is not as great as the difference in the body weights of the pythons, which ranged from 6 to 32 kg. This may possibly explain the differences in the two bases of comparison noted with these two species of animals. Further discussion of this point is left until all the cold-blooded animals are compared (pages 429 and 431).

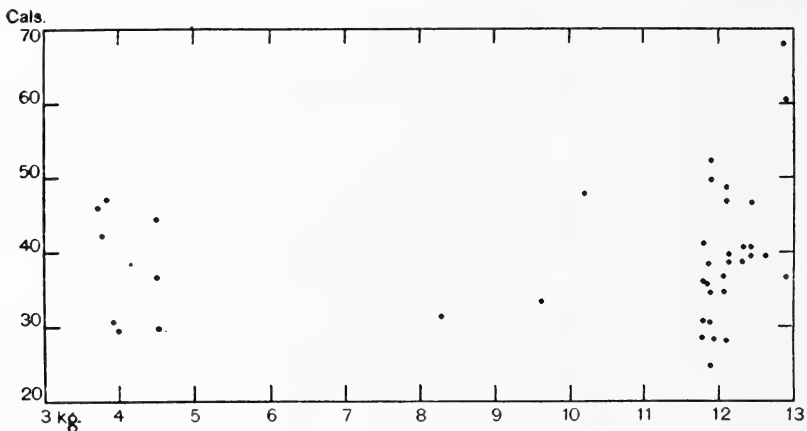


FIG. 62.—COMPARISON OF STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO BODY WEIGHT—BOAS WEIGHING ABOUT 4 AND 12 KG.

Environmental temperature in all these experiments was between  $27^{\circ}$  and  $29^{\circ}$  C.

The wide scatter of the points in figures 54 and 60, which contain the data for all the boas, is at first disconcerting. One should realize, however, that these charts, as presented, disregard two factors known, at least with warm-blooded animals such as humans, to affect metabolism, namely, age and sex. The weight factor has been ruled out by expressing the values per unit of weight. The calculation per unit of surface area automatically takes care of the height (length) and the weight factors. But age and sex have not been taken into account. Furthermore activity, although usually insignificant, certainly may have played a rôle in some of these experiments. The boas were all studied between 1915 and 1921. It was attempted to rule out periods of activity, but the true significance of seemingly small amounts of activity was not realized until perhaps the latest observations with the 1931 python. Before considering the distribution of the plotted points on these two charts as extremely irregular or anomalous, one should also recall that even with humans fully as great differences

can be expected in the measurements on a large number of individuals of the same size, weight, age and sex. For example, one has but to refer to the charts for children published by Benedict and Talbot,<sup>1</sup> to note equally as wide a distribution of plotted points. It is more than likely that if, in the case of these boas, activity, age, sex, and indeed, the kind and amount of food eaten and the length of fasting could have been definitely known, and if these factors could have been taken into account in the analysis of these two charts for all the boas, the distribution of the plotted points would be no greater than that found with other animals.

EFFECT OF EMACIATION ON SKIN AREA AND METABOLISM PER UNIT OF SURFACE AREA

Anybody who has seen how the skin of an emaciated snake hangs in great folds will be impressed with the belief that with the loss of body flesh there is no commensurate loss in skin area, because apparently there is no proportionate shrinking of the skin to correspond to the loss of

TABLE 59—*Effect of assumed shrinkage or non-shrinkage of skin during emaciation on metabolism of boa D per unit of surface area*

Date	Length of fast	Body weight	Calories per sq. m. per 24 hours		Environmental temperature
			Area shrinking with weight	Unchanged initial area of 0.69 sq. m.	
July 5-6, 1917	149 days	kg. 12.12	36.4	34.8	°C. 29.1
Apr. 5-6, 1918	1 yr. 58 days	8.16	63.2	46.7	32.0
June 27-29, 1918	1 yr. 141 days	6.69	62.9	40.1	30.0

tissue. Under the circumstances one should hold to the view that the skin area does not change with the state of nutrition and that the actual skin area of an animal that has fasted a long time and lost much weight is really much the same as when it was in a state of full nutrition. A calculation of the heat production per unit of surface area on this basis is therefore worthy at least of short consideration. The most striking instance we have of change in body weight is with boa D (table 33). The body surface of boa D, calculated by use of the constant 12.5 and on the assumption that the surface area changes with the weight, ranges from 0.69 square meter at the beginning of the series of experiments on March 15-17, 1917, to 0.44 square meter at the end of the series on June 27-29, 1918. For the last three experiments with boa D, when it weighed 12, 8 and 7 kg., respectively, we have computed the heat production per square meter of surface area (1) considering that the surface area decreased commensurate with the fall in body weight, and (2) assuming that the surface area did not change even with emaciation but remained at 0.69 square meter as at the start of the series. The results are given in table 59. In the first experiment, July 5-6, the surface area is 0.66 square meter, if

<sup>1</sup> Benedict, F. G., and F. B. Talbot, Carnegie Inst. Wash. Pub. No. 201, 1914, figs. 54, 56 and 58, pp. 152, 154 and 155.

calculated from the actual body weight on that date, and 0.69 square meter, if assumed to be unchanged since the initial weight of 12.96 kg. The heat production per square meter of body surface on these two bases is 36.4 and 34.8 calories, respectively, *i.e.*, no real difference. The most striking changes are to be expected in the experiments of April 5-6 and June 27-29, for the surface area computed from the actual weight is 0.51 square meter on April 5-6 and 0.44 square meter on June 27-29. In these two experiments the heat production on the basis of constant surface, that is, 0.69 square meter, is 46.7 and 40.1 calories, respectively, compared with 63.2 and 62.9 calories on the basis of a shrinking surface area. If one examines figure 58, in which the heat production per square meter of body surface is referred to environmental temperature with boa D, it can be seen that the two plotted points for the long fast of 1 year and 58 days and 1 year and 141 days lie above 60 calories. If calculated on the assumption that the surface area does not decrease with emaciation, they would lie at 47 and 40 calories, respectively. In other words, these points would be brought down very close to the six experiments between 28° and 30° C. But there still remain the aberrantly high points for the group of experiments at about 29.8°, which are unaffected by emaciation and therefore can not be corrected to a lower level. Hence the picture is not at all clarified by the assumption of a uniform skin area with emaciation.

In calculations for boa M of the metabolism per unit of surface area (table 44, p. 180), the surface area was considered to vary with the weight. On the assumption that the maximum or initial surface area, 0.32 square meter, is unchanged although there is a fall in body weight from 4.06 to 3.41 kg., or 16 per cent, we find that the heat production per square meter of surface area in the experiment of February 10-13 is 17.6 calories instead of 20.1 calories, as computed by assuming the area decreases with the weight. The heat production in the experiment of December 30 to January 2, when the body surface was 0.32 square meter by either assumption, was 20.8 calories. Since both the February and the January experiments were made at 21° C., it can be seen that the assumption of no shrinkage in area in the February experiment gives a wider difference between the metabolism values for the two experiments than would be the case if the area were considered to decrease commensurate with the weight. Hence the assumption of no shrinkage in area does not better the picture.

A similar comparison may be made for the small Indian python, the body weight of which ranged from 7.43 kg. on April 8-9, 1916, to 6.00 kg. on December 6-7, 1916, and 5.89 kg. on October 28-29, 1916. Using the maximum surface area as 0.47 square meter, we calculate that the standard heat production is 25.4 calories per square meter of body surface on December 6-7 and 20.4 calories on October 28-29, as against 28.4 and 23.4 calories, respectively, if the area is considered to decrease with the weight. In other words, assumption that the skin area does not shrink with loss of flesh gives differential results identical with those obtained by using the surface area computed from the reduced weight.

## COMPARISON OF HEAT PRODUCTION OF GOPHER SNAKES

## HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT

Although only four average values are available representing the standard heat production per kilogram of body weight of gopher snakes (see table 47, p. 184), these values have been plotted with reference to environmental temperature in figure 63. It will be recalled that of these four experiments only one was made with a single gopher snake (represented by a cross in fig. 63) and the others were made with groups of three snakes (represented by dots). Influenced by our experience in the charts for the other snakes, from which we found that a straight line rarely represents the trend of the metabolism, we have sketched a curve through these four points more or less characteristic of the curves noted with the snakes

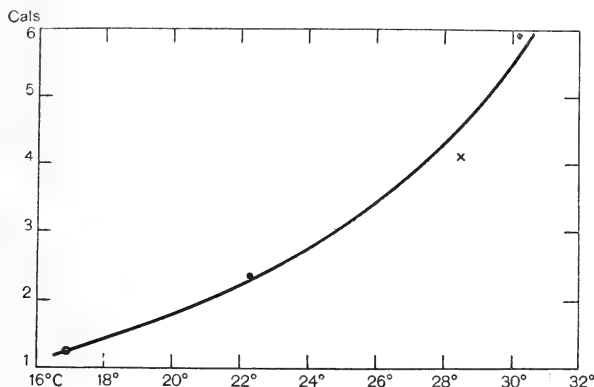


FIG. 63—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—GOPHER SNAKES.

Cross represents an observation upon a single gopher snake; dots represent observations on a group of three gopher snakes.

already discussed. At 28.5° C. the plotted point represents the measurement with a single gopher snake, which weighed half the total weight of the group of 3 snakes used in the other experiments. Although there is a tendency for snakes to have a slightly higher metabolism when studied in a group than when studied individually, we feel justified in leaving this point on the chart and letting it influence slightly the general course of the curve. The usual trend indicating an increase in metabolism with increase in environmental temperature is apparent.

## HEAT PRODUCTION PER SQUARE METER OF SURFACE AREA

The few values available for the standard heat production of gopher snakes per square meter of surface area are plotted with reference to environmental temperature in figure 64, the cross again indicating the single snake and the dots the groups of three snakes. Care was taken not to compute the surface area of the groups of three snakes from the total weight of the group, but to calculate the area of one snake from one-third of the total weight of the group (it would have been preferable to know



the actual individual weights) and then multiply that by the number of snakes in the group to get the total body surface. With the first group of three snakes studied on January 2 to 6, 1917, for example, the total body weight was 5.76 kg. If the body surface were calculated from the two-thirds power of this total weight multiplied by 12.5, the area would be 0.40 square meter. But if the weight of a single snake is accepted as equal to 1.92 kg., that is, one-third of 5.76 kg., calculation shows that the area of a single snake weighing 1.92 kg. is 0.19 square meter and hence the total area of the three snakes is equivalent to 0.57 and not to 0.40 square meter. It is realized that the total surface thus computed was not entirely

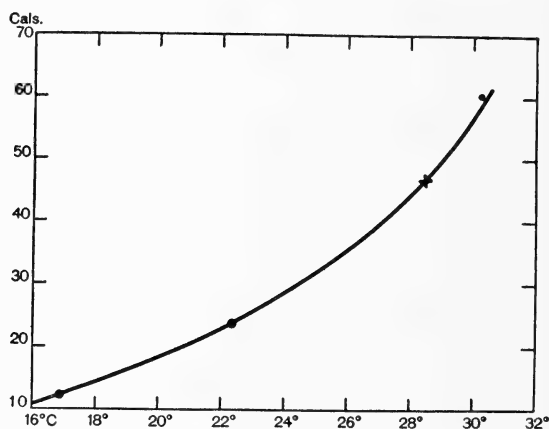


FIG. 64—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—GOPHER SNAKES.

Cross represents an observation upon a single gopher snake; dots represent observations on a group of three gopher snakes.

exposed to the air, for the surface area of the group as such more closely approximates a real sphere than perhaps the individual snake itself, because there will be more intertwining.

Since there were no great differences in the weights of these gopher snakes, the similarity in the general pictures shown by figures 63 and 64 is what would be expected. In both charts there is a regular grouping of the plotted points about the general curve. From this rather crude inspection it would appear as if the reaction of the standard metabolism of the gopher snake to environmental temperature is uniform, whether considered upon the basis of heat production per kilogram of body weight or per square meter of body surface, and that it is justifiable in both cases to draw a general curve showing the trend of the metabolism.

#### COMPARISON OF HEAT PRODUCTION OF RATTLESNAKES HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT

Strictly speaking, our measurements of the rattlesnakes studied individually and in pairs should be discussed separately. To simplify matters,

we have used the data in table 50 (p. 191) and have plotted in figure 65 the standard 24-hour heat production per kilogram of body weight referred to environmental temperature, both for the pairs of rattlesnakes (represented by dots and hollow squares) and for the individual rattlesnakes A, B, C and D (represented by crosses). Since the observations with individual rattlesnakes were made at much higher temperatures than those with the pairs of rattlesnakes, this use of the material in figure 65

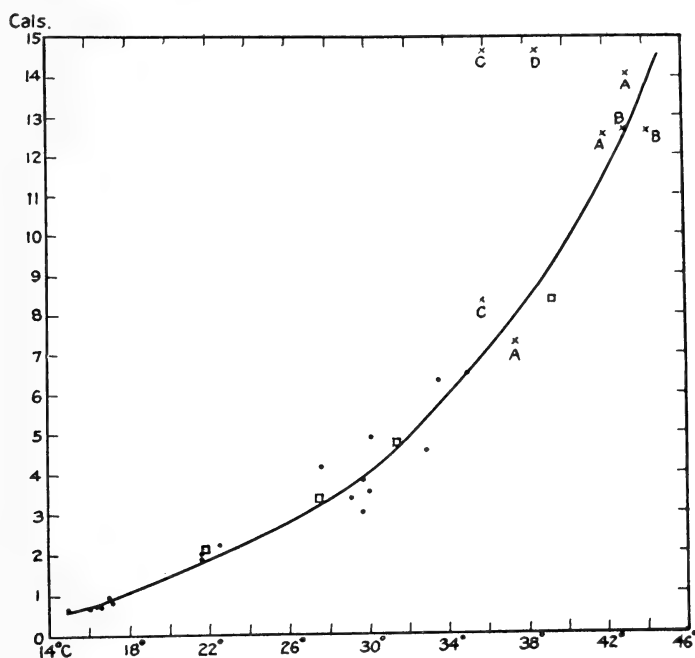


FIG. 65—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—RATTLESNAKES.

Dots represent observations on pairs of rattlesnakes weighing together about 10 kg. Hollow squares indicate observations on pairs of rattlesnakes weighing together about 6 kg. Crosses represent observations on individual rattlesnakes, A, B, C and D, weighing from 2.5 to 5 kg. each.

is especially justifiable. Except for two values with rattlesnakes C and D at 36° and 38.6° C., respectively, all the plotted points lie reasonably close to the curve representing the general trend of metabolism. Indeed, with the rattlesnakes there is a far closer semblance of uniformity than was found with any of the boas.

Rattlesnakes C and D require special consideration. By reference to table 49 it can be seen that on the day the high value was obtained with snake C (June 29, 1917) the animal probably was over-heated, as it died sometime during the 10 hours of experimentation following the first period. In the experiment with rattlesnake D which gave the high heat production (July 1-3) there were, after the first period of adjustment, five

fairly uniform periods, but the metabolism steadily increased thereafter and the rattlesnake died during the experiment, probably during period 10. In other words, these two high values were obtained with animals that were definitely abnormal. Probably they could not lose any heat and were in a distinctly febrile condition.<sup>1</sup> We have therefore disregarded these two values in laying the curve on this chart.

The standard heat production of rattlesnakes A and B at the temperatures of 42° to 44° is strikingly high, from 12.5 to 14 calories per kilogram of body weight per 24 hours. When it is realized that the adult human with a rectal temperature of 37° C. produces approximately 25 calories per kilogram of body weight per 24 hours at rest and in the post-absorptive state, it can be seen that the rattlesnake at 42° to 44° C. has a metabolism per kilogram of body weight somewhat more than half as great as that of man at 37° C. The adequate control of the environmental temperature of these snakes in a respiration chamber is a problem. What the ventilation rate should be and what the degree of humidity inside the chamber should be for the ideal loss of heat is as yet unknown. It is not impossible that in the case of the high values found with rattlesnakes C and D, the ventilation rate was too low and that the vaporization of water was hindered and thus the high metabolism resulted. In the case of the two experiments with rattlesnake B, which were at the highest temperatures of all, practically 44° C., the animal survived the first day and on the next day, nearly 24 hours later, gave essentially the same value for standard metabolism as on the day before. But it died during the second experiment, unquestionably from inability to lose its heat properly. The plotted points in figure 65 are sufficiently well clustered about the curve, however, to indicate that the probable standard heat production at temperatures of from 42° to 44° is not far from 13 calories per kilogram of body weight per 24 hours. Although the exact location of this curve may be debatable, it does represent the probable general trend and is important here in showing the comparatively small deviation of individual points from the general trend and for comparison subsequently with the general curves for other large cold-blooded animals. The four points represented by hollow squares are for pairs of snakes weighing about 6 kg. These data are especially discussed in the following consideration of the heat production per unit of surface area.

#### HEAT PRODUCTION PER SQUARE METER OF SURFACE AREA

The heat production per square meter of body surface of these rattlesnakes was computed in the usual way and has been plotted in figure 66, the dots and hollow squares again indicating pairs of snakes and the crosses individual snakes. The curve sketched on this chart gives a fair representation of the general trend of the metabolism, with only occasionally aberrant points, most of which appear at the higher temperatures. The two unusually high points for rattlesnakes C and D, which were discussed in the preceding chart, have been left in figure 66, although

<sup>1</sup>Rubner (*Kraft u. Stoff im Haushalte der Natur*, Leipzig, 1909, p. 91) has pointed out the abnormally high metabolism of frogs heated to 37°.

they have been disregarded in laying on the curve. Since it has been the custom for investigators to study cold-blooded animals at much lower temperatures (in the neighborhood of  $16^{\circ}$  to  $20^{\circ}$  C.) than those at which many of these experiments with rattlesnakes were made, it was one of the functions of this research to extend the measurements on cold-blooded animals into a higher temperature field. The rattlesnakes alone of all the snakes were able to withstand the high temperatures, although even

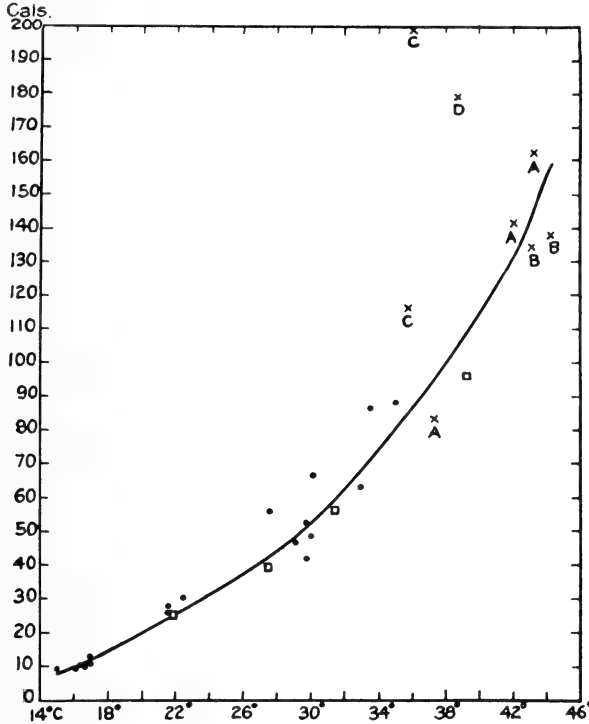


FIG. 66—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—RATTLESNAKES.

Dots represent observations on pairs of rattlesnakes weighing together about 10 kg. Hollow squares indicate observations on pairs of rattlesnakes weighing together about 6 kg. Crosses represent observations on individual rattlesnakes, A, B, C and D, weighing from 2.5 to 5 kg. each.

these snakes finally died (either during or after the experiment) when subjected to temperatures as high as  $39^{\circ}$  to  $44^{\circ}$  C. The same difficulty in comparing the relative merits, as regards uniformity in metabolism, in the expressions of the heat production per kilogram of body weight and per square meter of body surface that was noted strikingly with the boas appears here likewise with the rattlesnakes. From crude inspection of figure 66 there seems to be little, if any, advantage in the expression on the basis of surface area. More than half of the observations were made with a pair of rattlesnakes weighing together about 10 kg. Three

points below  $32^{\circ}$  and one at  $39^{\circ}$  were obtained with pairs of snakes weighing only 5.88 and 5.94 kg., respectively. On the supposition that the surface-area expression would wipe out inequalities in size better than the body-weight expression, we have indicated by small squares on the chart those points dealing with these *pairs* of *small* snakes. We have likewise indicated the points for individual rattlesnakes A, B, C and D. Hence those points not marked are for the *pair* of snakes weighing 10 kg. With observations on animals weighing twice as much as other animals, the possibility of an influence of the surface area must be considered.

The heat production per kilogram of body weight (fig. 65, p. 239) of the pair of small snakes weighing 5.88 kg. is close to the general curve in all three cases. All three points are slightly above the general curve. In the chart for the heat production per square meter of body surface (fig. 66) likewise all three points lie reasonably close to the curve, but two lie somewhat below it. From the inspection of the curves in figures 65 and 66, and in lieu of any more subtle mathematical analysis, one is not justified in concluding that the method of calculation on the basis of surface area gives a more uniform picture than that on the basis of body weight. Little comparison can be made of the individual snakes at the higher temperatures, owing to the already noted great lability of the metabolism at these temperatures and because undoubtedly the factor of pyrexia entered into some of these experiments.

The heat production per square meter of surface area at a temperature of  $36^{\circ}$  and  $38.6^{\circ}$  rises to 199 and 179 calories, respectively, with snakes C and D, which died as a result of overheating. With the other single snakes the highest recorded heat production is 163 calories. All of these snakes, when measured at or above  $40^{\circ}$ , and one when measured at  $36^{\circ}$ , died. With snakes A and B duplicate experiments on different days were made and values essentially the same were found showing that, at least at the time the first of these two experiments was made, the animal had not been permanently or seriously damaged. The activity of these animals, when they were combatting the high temperature and the high humidity, undoubtedly was a notable factor. We are quite in accord with the belief that these cold-blooded animals should not be heated above  $40^{\circ}$  for any length of time, but we are convinced that with low humidity they may safely be heated to  $37^{\circ}$ , and that the metabolism of these snakes at  $37^{\circ}$  (*i.e.*, the temperature of man) is perfectly comparable with that of other cold-blooded animals at this temperature. The general regularity in the trend of these curves as a whole suggests strongly that from measurements made at  $30^{\circ}$ , or below, the metabolism may be reasonably well projected to  $37^{\circ}$  (in default of actual measurements at  $37^{\circ}$ ) without serious error. This procedure has been used in the comparison of the metabolism of cold-blooded and warm-blooded animals on pages 501 to 506.

#### COMPARISON OF STANDARD METABOLISM OF SNAKES OF DIFFERENT SPECIES

With as varied a lot of snakes as were used in our observations on gaseous metabolism, ranging from the 32-kg. python down to an indi-

vidual gopher snake weighing 2.4 kg. and comprising in all 34 snakes (3 pythons, 14 boas, 7 gopher snakes and 10 rattlesnakes), a comparison of the metabolism of the different species of snakes is justifiable. Such comparison, because of the great variation in the body weights of these snakes, must be made upon the basis of the heat production per kilogram of body weight as well as that per square meter of surface area. In figure 67 the four curves representing the general trend of the standard metabolism per unit of weight with increasing environmental temperatures have

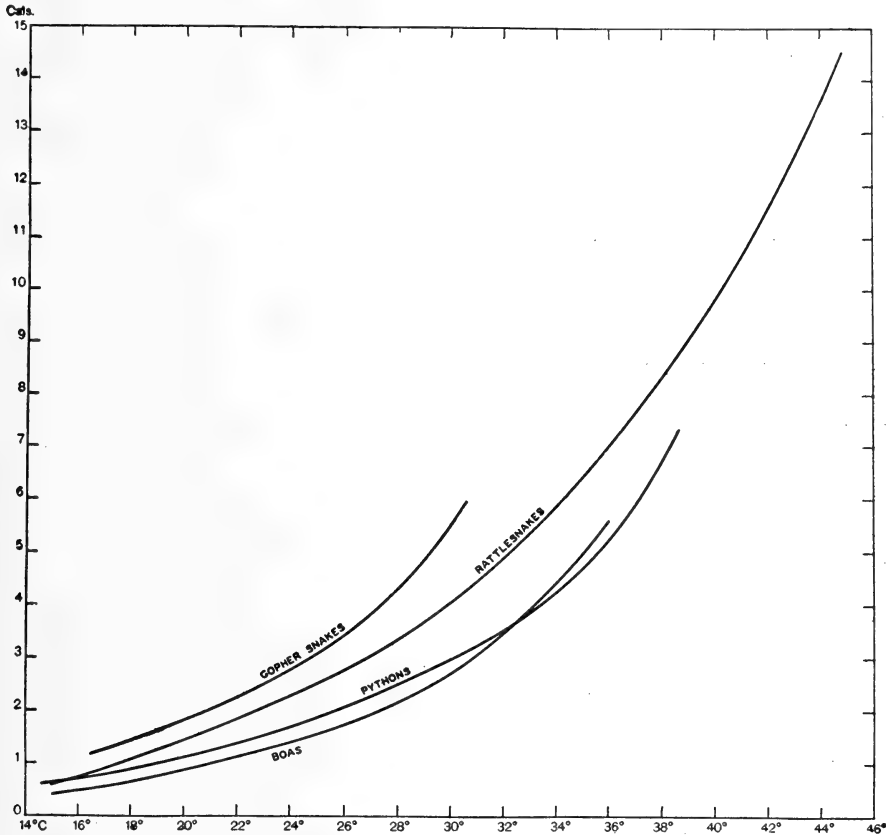


FIG. 67.—COMPARISON OF STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—ALL SNAKES.

been replotted for pythons, boas, gopher snakes and rattlesnakes, respectively. These have been taken directly from the composite curves already shown for each species of snake (figs. 48, 54, 63 and 65). Sufficient emphasis has been laid in the earlier discussion upon the great deviation of the individual points and the consequent difficulty in laying on these charts *any* curves representing the general trend of metabolism. Since, however, these curves have been drawn, we may with these reservations in mind compare the *general trend* of the standard heat production of the various species of snakes, referred to the environmental temperature and corrected to a common unit of body weight.

For the rattlesnakes, our curve extends from 15° to 44° C. Since the curve for the gopher snakes does not extend beyond 32° C., however, the comparison of all the different species can not be made beyond this temperature. Nevertheless the rattlesnake curve has been plotted for its entire length in figure 67, as giving the greatest extremes in temperature. The metabolism of the gopher snakes remains continually at the highest level of all the snakes. The metabolism of the boas remains consistently at the lowest level. The curve for the pythons for the greater part parallels that for the boas, being somewhat above it and crossing the rattlesnake curve at 16° C. The parallelism between the curves for the boas, pythons, and rattlesnakes is, to say the least, striking, although the levels are markedly different in the three families. The curve for gopher snakes runs reasonably parallel with the other curves up to 28°, but there is a marked rise in the next three degrees. The divergence of the curve for gopher snakes (our smallest snakes) is probably a real fact, representing the highest heat production per kilogram of body weight of all the species at the temperatures indicated. This curve, however, is based upon only four measurements, three with three gopher snakes in the chamber at one time and one with one snake.

The difficulty of drawing any of these curves, especially for the individual snakes, has been continually emphasized, and although we have ventured to lay on curves typifying the *general trend* in metabolism for the individual snakes and for each separate species of snake, it does not seem justifiable to lay on a general curve here in figure 67 representing *all* the snakes. From a rough inspection of the chart it would appear that if such a curve were laid on, it would probably lie not far from that represented by the curve for rattlesnakes. The fact that the four species of snakes could give general curves of such parallel nature, although differing in absolute level, is striking when one considers the great deviation found in the individual points on the curves for the different groups, especially the boas. If one were to compare these species of snake on the basis of average weight, one would consider the pythons as weighing the most (this group being made up of only three snakes, one of 32 kg. and two of from 5 to 7 kg.), the boas on the average next, the rattlesnakes next, and the gopher snakes lowest. According to these average weights the standard heat production per kilogram of body weight is lowest with the largest snakes, although the curve for the pythons does actually lie somewhat above that for the boas.

It has already been pointed out that it is only with the pythons and the boas that one can expect, owing to striking differences in body weight, to find any material alteration in the general picture when computations are made on the basis of surface area. Hence no comparison of the two bases of calculation is stressed with the rattlesnakes or with the gopher snakes. With the boas there was certainly no distinct advantage in favor of the heat production per square meter of surface area. A comparison, however, of the heat production per square meter of body surface of all the different species of snakes, as given in figure 68, presents a most interesting picture, in that the curves representing the *general trends* for the

four species of snake lie astonishingly close. Here one would be justified in laying on a curve showing the average heat production per square meter of body surface of snakes in general. In order, however, not to confuse the picture but to make it possible to single out easily the individual

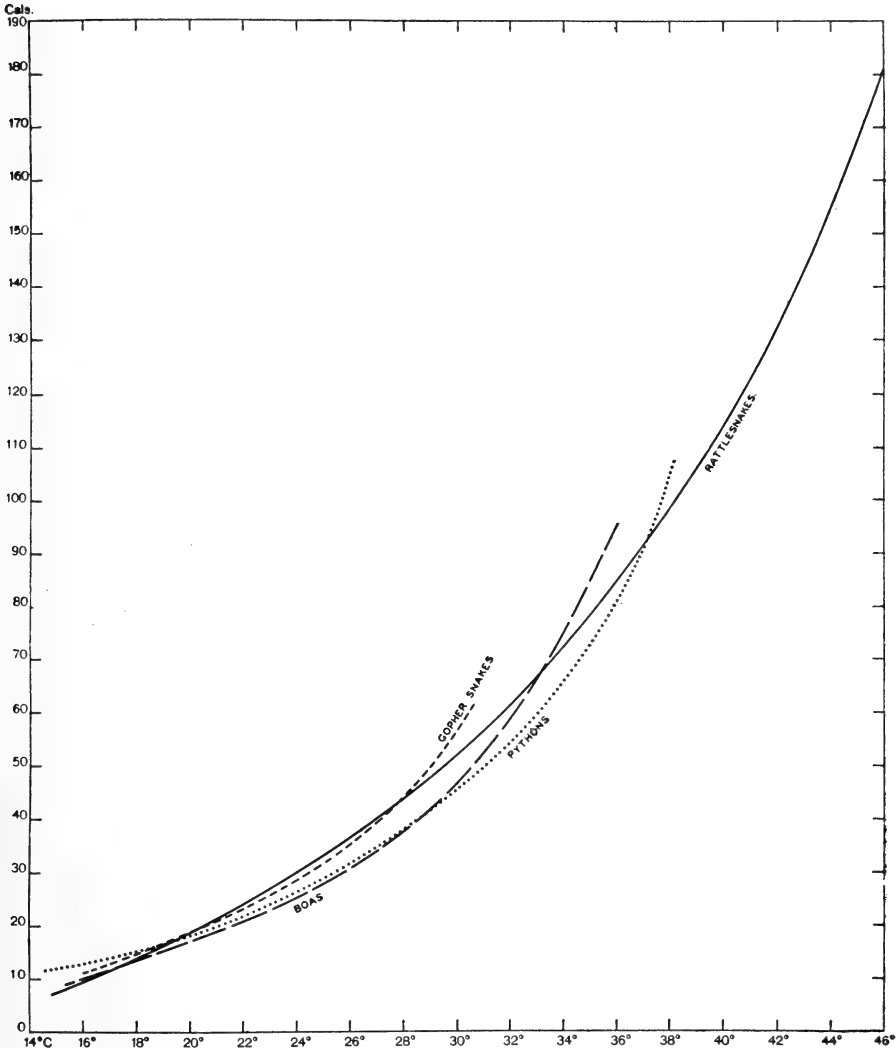


FIG. 68—COMPARISON OF STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—ALL SNAKES.

species, such a curve has not been placed on the chart. A moment's comparison of figures 67 and 68 shows the striking uniformity among the different species of snakes in the general trend of the heat production per



square meter of surface area,<sup>1</sup> as compared with the general trend of the heat production per kilogram of body weight.

The general uniformity of these curves is of itself a fairly good argument for the propriety of putting on the curves for general trends and for the probable accuracy of the curves as drawn. It is clear here that no plateau in metabolism is to be found and that there is a continual increase in metabolism with increasing temperature. Comparison of the divergence of the curves in figure 67 with the extraordinary uniformity of most of the curves in figure 68 leaves no doubt but that the expression of the heat production per square meter of surface area gives the most uniform results with these four species of snake. In view of the great differences in size between the small gopher snakes and the giant python, figure 68 taken by itself could be used as an admirable indication of the applicability of the surface-area law to snakes of greatly varying body weights. Consideration of the extent to which the surface-area law may be applied to all cold-blooded animals must be left until the comparison is drawn of all the different groups of cold-blooded animals (see pages 470 to 473).

Buytendijk,<sup>2</sup> in 1910, reported observations on the metabolism of fast-ing snakes, varying from a *Coronella austriaca* of 24.8 grams to a boa of 2830 grams. Their metabolism was measured only at 19° and 20° C. At 19° the heat production per kilogram of body weight of our large snakes (fig. 67) varied on the average from 0.75 to 1.60 calories. If an average value might be taken, it could be assumed to be 1.2 calories. With the snakes of Buytendijk we have calculated that the heat production per kilogram of body weight per 24 hours (assuming a respiratory quotient of 0.72) ranged from 5.02 to 67.7 calories, at 19° C. If the small snakes are disregarded and only the boa constrictors that were approximately the size of some of our snakes are considered, the heat values are 8.23 calories for a boa weighing 810 grams and 5.02 calories for one weighing 2830 grams. These values are four to seven times greater than the average value for our snakes in general. Even our smallest snakes, the gopher snakes, which more nearly approximated the weight of Buytendijk's boas, produced only 0.75 calorie at 19° or one-ninth of the average heat production of his boas. Precisely the same differences are to be found, as is to be expected, in the metabolism of these snakes expressed on the basis of the body surface. Thus, our snakes in general at 19° produced not far from 17 calories per square meter of body surface, whereas Buytendijk's snakes produced from 57 to 194 calories, the larger animals producing 57 and 61 calories, respectively, or three to four times the values found with our snakes as a whole.

<sup>1</sup>Baldwin (Proc. Iowa Acad. Sci., 1930, **35**, p. 318), working with bull snakes at 20°, ranging in weight from 422 grams to 822 grams, is inclined to the belief that, although at first sight his figures seem to indicate that the law of surface area might apply, the individual differences were so varied that no causal relation between surface area and energy exchange can be drawn.

<sup>2</sup>Buytendijk, F. J. J., Proc. Section of Sc., Royal Acad. Sci., Amsterdam, 1910, **13**, p. 48; *ibid.*, Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd., 1910, **18**, p. 870.

## GASEOUS METABOLISM AND ENERGY TRANSFORMATIONS OF SNAKES DURING DIGESTION

With warm-blooded animals, particularly dogs and man, innumerable studies have been made on the influence of digestion. Rubner was the first to point out quantitatively the great increase in metabolism following the ingestion of food and laid down his laws with regard to the specific dynamic action of foodstuffs. Although Rubner was very explicit in his definition of "specific dynamic action," this expression has been used, in a far more general way by all writers ever since, to indicate apparently on any scale whatsoever the increase in metabolism following food ingestion. Emphasis is usually laid on protein ingestion. The effect of such ingestion may be studied, in the first place, from the standpoint of the "peak effect," that is, the maximum increment in metabolism above the basal heat production following the food ingestion. The measured peak effect has been especially used by clinicians in studying the influence of food. In the second place, the effect of food ingestion may be measured in terms of the entire excess heat produced above the basal heat production as a result of the ingestion of the food. This excess heat production may, in turn, be referred either to the basal metabolism per 24 hours or to the energy value of the digestible nutrients in the food. For purposes of discussion we will consider the influence of the ingestion of food from the standpoint of the peak effect and, in certain experiments, the total increase in metabolism caused by the ingestion of food referred to the digestible calories in the food. Admittedly this last calculation is difficult, for true digestion experiments with the snake are missing. But on the assumption that approximately 90 per cent of the energy ingested would be digested, this calculation has tentatively been made. This last comparison has been expressed by the term "cost of digestion," used by Benedict and Carpenter.<sup>1</sup> It is obvious that with cold-blooded animals (regarding the character of the digestion of which so little is known and the metabolism of which during digestion has hardly been studied) fine differentiations as to the effect of protein from the quantitative standpoint can hardly be expected.

Special attention was paid to the influence of protein, inasmuch as this is the natural food of the dog, the animal first extensively used in these digestion studies. With the dog and with man much the same picture has been obtained, that is, an increase in heat production due to the ingestion of food, this increase being highest after protein and much lower after fat and carbohydrate. The explanations of this increased metabolism have varied greatly and have been the basis of much discussion, dominated in large part by the fundamental idea that the greatest increase occurs after the ingestion of protein. In recent years the situation has been complicated somewhat more by the emphasis laid upon the fact that with ruminants the ingestion of a protein-poor hay produces an increase in metabolism comparable to that caused by the ingestion of pure protein

<sup>1</sup> Benedict, F. G., and T. M. Carpenter, Carnegie Inst. Wash. Pub. No. 261, 1918, p. 335.

with dogs and with man.<sup>1</sup> In the field of cold-blooded metabolism little research on this problem has been carried out with the larger animals. It has been noted that immediately after food, the metabolism is higher than after prolonged fasting. Studies of the effect of food with snakes or other large cold-blooded animals differ appreciably from those with warm-blooded animals in which the period of fasting prior to giving the food is usually short, so short as to have no material influence upon the composition of the body as a whole. The cold-blooded animal, such as the snake, frequently experiences prolonged fasting, and when food is finally ingested, it may represent at the time a considerable percentage of the animal's body weight. In such cases there will be not only a stimulus to metabolism due to the food, but large amounts of both protein and fat may be *deposited* in the body. Thus the food will serve to meet all the animal's energy needs for several weeks and sometimes months. Digestive activity *per se* is a response to ingested food, a response that is almost immediate, rather intense and, certainly with warm-blooded animals, ordinarily disappears rapidly. With man the digestive processes persist usually for not more than 12 hours, with dogs and some other warm-blooded animals rarely more than 24 hours, and with ruminants from 36 to 48 hours. On the other hand, extreme undernutrition resulting from prolonged fasting is accompanied by a complete change in body composition. In studies with cold-blooded animals, whose metabolism is always at a low ebb, it is difficult to differentiate between the stimulus due to food and the possible effect of recuperation following prolonged undernutrition. With many of the large cold-blooded animals that we studied, the exact time since last feeding was uncertain, and it is not impossible that at times the animal had undergone a long period of fasting with changes in body composition. In only one case, however, was the snake (boa D) so far advanced in undernutrition as to show definite signs of emaciation.

In the literature, the only specific instance of studying the metabolism of snakes or other cold-blooded animals of large size after food is the investigation of Buytendijk.<sup>2</sup> A boa constrictor, weighing 2830 grams, gave off 32 c.c. of carbon dioxide per kilogram of body weight per hour at 19° C., when without food. It then ate a pigeon, probably (although not stated) a common pigeon weighing not far from 350 grams. After 4 hours the carbon-dioxide production had increased to 52.9 c.c., although there was a slight rise in environmental temperature to 20.5° C. After 52 hours it was 49.4 c.c. and after 124 hours 55.5 c.c. No results are reported beyond this time. With a second boa constrictor, weighing 3123 grams, apparently the metabolism prior to food ingestion was not determined. Since its weight was but slightly greater than that of the first boa, one can argue that probably the production of carbon dioxide unaffected by food ingestion was not far from that of the first animal, that is, 32 c.c. per kilogram of body weight per hour. This boa ate 2

<sup>1</sup> Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. 377, 1927, pp. 223 *et seq.*

<sup>2</sup> Buytendijk, *loc. cit.*

rats, and three experiments at 19° C. were made 2, 24 and 48 hours after eating. At these times the carbon-dioxide production was 41.5, 42.5 and 52.9 c.c., respectively. Buytendijk concludes that the influence of alimentation on the metabolism of the boa constrictor is perceptible but not so great as would be expected.

During the progress of our observations on the standard metabolism of large snakes, the opportunity was taken on many occasions to study the course of the carbon-dioxide production following the ingestion of food. These measurements were continued without interruption until after the maximum increase in metabolism had taken place and in some cases until the metabolism had returned to the pre-digestive level. In these digestion experiments, the effects both of protein and of fat were studied and at different environmental temperatures. The protein meal consisted of a rabbit or a guinea-pig and in one instance of sparrows. The fat meal was composed of beef fat wrapped in the pelt of a rabbit or a guinea-pig. The snake was frequently placed in the respiration chamber before the animal was given to it, and hence did not have to be handled or transported before the respiration experiment began.

In computing the heat production from the measured carbon-dioxide production in the digestion experiments with beef fat, the respiratory quotient was assumed to be 0.72. In the protein experiments obviously the assumption of the respiratory quotient for fat would be unjustifiable. Since animal food was given to the snakes, a minimum amount of carbohydrate was ingested and the meal consisted practically of a mixture of protein and fat. The exact proportions of protein and fat eaten are not known, save that the rabbit or guinea-pig given to the snake was not excessively fat. Since the respiratory quotient of pure fat is 0.71 and that of pure protein is 0.81, it seems justifiable to assume that the average respiratory quotient during the protein experiments would be 0.76. In this belief we are supported by an analysis made of the body of a rabbit (see page 300). Theoretically, the respiratory quotient would fall off gradually after the ingestion of animal food until the post-digestive state is reached, when it would again be about 0.71, and at the peak of digestion it might be higher than 0.76. Undoubtedly the respiratory quotient does not remain constant at 0.76 throughout the entire period of digestion of protein and suddenly drop to 0.71 after the period of digestive activity has ceased. But the error involved in computing the heat production from the carbon-dioxide production whether the quotient is 0.71 or 0.76 is at the most only 6 per cent, and we have therefore adopted the perhaps illogical procedure of using a quotient of 0.76 throughout the entire period of protein digestion. Ideally, the respiratory quotient should have been determined continuously throughout the entire digestive cycle, and changes in the caloric value of carbon dioxide made as the measured quotient changed. Our technique at the time did not permit this. But the increment in heat production following food ingestion was found to be so great that for general comparison of the metabolism during digestion with that under standard conditions one can disregard the possible difference of

6 per cent in the caloric value of carbon dioxide when considering the computed heat values for the protein experiments.

In the following tables in which the results of the digestion experiments with snakes are reported, the time since eating represents the time up to the beginning of the experimental period. In most instances the periods were consecutive, without any interruption. In these instances the period number is given, and the length of the period can be calculated, if desired, from the column for "time since eating." In a few instances the periods were not consecutive, as with the small Indian python in the experiment of March 10 to 15. In these cases a column has been included in the table for "length of period." The body weight was determined at the start of each digestion experiment and, as recorded in the following tables, *includes the weight of the food eaten*. It was likewise determined at the end of the experiment after the snake had been removed from the respiration chamber, in some instances directly afterward, and in other instances at an unknown time afterward. In the calculation of the carbon-dioxide production and the heat production per kilogram of body weight for each period of the digestion experiment it was assumed that the body weight decreased gradually, that is, approximately 0.01 or 0.02 kg. for each few periods, according to the total length of the experiment and the total loss in body weight during the experiment. The actually determined initial and final body weights are recorded usually in the footnotes in the following tables, but it is not believed necessary to give the details regarding the assumed decrease in weight during the progress of the experiment.

The environmental temperature was held practically constant throughout each digestion experiment. The average environmental temperature is shown just below the title of each table, together with the kind and amount of food ingested and the date when food was eaten. The snakes were, as a rule, quiet in all the digestion experiments, but any measurement affected by activity will be specially commented upon. In these digestion experiments the values for carbon-dioxide production and heat production will always be expressed as grams or calories *per kilogram of body weight per 24 hours*. For the sake of brevity, in discussing the results in the text we shall speak of the values only as grams or calories, without repetition each time of the fact that they have been computed for definite units of weight and time.

The standard metabolism values that seem best suited for comparison with the digestion experiments are underlined in the tables, immediately preceding the data for the particular digestion experiments to which they apply. These underlined values will be referred to in the following discussion as "baseline" values, but are not to be interpreted as representing the "basal metabolism" as that expression is ordinarily used. They simply afford a basis for comparison of the metabolism during digestion with the metabolism obtaining under the standard conditions outlined on page 155. In deciding what baseline values should be used for comparison with the digestion experiments, we have, whenever possible, made use of standard metabolism measurements obtained on the snakes

shortly before the digestion experiments and made at the same environmental temperature as the digestion experiments. When such data were not available, the baseline value was derived from the smoothed metabolism curve for the individual animal under study or from the average curve for all the snakes of the particular species. When the actually determined standard value was obtained at a temperature somewhat above or below the temperature of the digestion experiment, it has been "corrected" to the temperature of the digestion experiment according to the percentage change in metabolism with changing temperature indicated by the curve for the individual snake or by the general curve for the species. When the standard metabolism was not directly determined, the baseline value has been drawn from the curve for that particular snake, and when no general curve for the individual snake was available, the general curve for the entire species has been used to approximate the baseline for calculating the increase in metabolism due to the ingestion of food. This latter procedure is distinctly open to criticism, for throughout this report emphasis has been laid upon the uncertainty of drawing a smoothed curve on any of the charts to show the general trend of the metabolism with increasing temperature, especially in the case of the boas, where a wide deviation in the individual measurements was noted. The uncertainty of employing a general curve to predict the metabolism of an individual snake is fully recognized. But in some instances the baseline values for comparison with the digestion experiments could be derived only in this way. Hence in the following discussion, although the increase in metabolism due to the ingestion of food has been calculated as the percentage increase above the "baseline," it should constantly be borne in mind that these percentages are only approximate.

### METABOLISM OF SNAKES DURING DIGESTION OF PROTEIN

#### SMALL INDIAN PYTHON

Fortunately a few of the snakes that were available for our observations were (to use zoological park parlance) "good feeders," particularly the small Indian python and some of the boas. With these snakes, the weight of food given and the time of eating were noted and the metabolism was studied during digestion at various environmental temperatures. The first measurements were made with the small Indian python, the standard metabolism of which has already been reported (see pages 192 to 201). The results of the protein digestion experiments with this python are given in tables 60 to 67.

#### PROTEIN DIGESTION AT ABOUT 28° C.

In the first protein digestion experiment in March 1916, the environmental temperature averaged 28° C. The python ate a rabbit on March 9 and was put into the respiration chamber on March 10. It had previously fasted for about 5½ months, during which time the standard carbon-dioxide production was measured twice (on February 2-3 and February 4-5) at an average temperature of 29.3° C. and was found to average 0.631 gram. In order to compare this standard metabolism with the metab-

olism during the digestive period, it is necessary to correct for the difference in environmental temperature between the two experimental series. Fortunately in our general curve in figure 45 (p. 199) we have a reasonably close picture of the metabolic trend of this python with changing temperatures. In correcting for the difference in environmental temperature, we may justifiably make use of this curve for this snake and similar general curves for the other snakes, rather than to apply some general average percentage value. According to the general curve in figure 45 indicating the course of the standard metabolism during the *prolonged* fast of this python, the standard metabolism at 28° C. (that of the first digestion experiment) would be about 10 per cent lower than that at 29.3° C. The standard carbon-dioxide production of 0.631 gram at 29.3° C. should therefore be reduced to 0.568 gram (1.89 calories) for comparison with the values found during the March digestion experiment (table 60). This com-

TABLE 60—*Metabolism of small Indian python during protein digestion*  
(28.0° C.; 765-gm. rabbit eaten Mar. 9)

Date	Body weight	Time since eating	Length of period	Per kg. per 24 hours	
				Carbon dioxide	Heat produced
1916 Feb. 2-5	kg. 6.95	days hrs. 128	hrs. ....	gm. <sup>1</sup> 0.568	cal. <sup>1</sup> 1.89
Mar. 10-11	7.68	22	16	2.834	9.02
Mar. 11-12	7.63	2 2	13	4.421	14.07
Mar. 13-14	7.57	3 22	17	1.518	4.83
Mar. 14-15	7.54	4 21	20	1.114	3.55

<sup>1</sup> Corrected from 29.3° to 28.0° C. See page 251.

parison shows that 22 hours after the python had eaten a 765-gram rabbit equivalent to 11 per cent of its initial weight (less the food eaten), there was an enormous increase in the carbon-dioxide production (five times that of the standard metabolism) during a period of 16 hours. On the next day the increase was even greater. The metabolism then began to decrease, but on March 14-15, when the experiment ended, it was still nearly double the standard metabolism.

The few values for the metabolism of the small python during this first digestion experiment are shown graphically in the lower half of figure 69, expressed in calories and referred to days since eating. On this same chart the standard heat production, which is recorded in table 60 for comparison with the results of this particular digestion experiment, has been indicated as a straight line, representing the baseline of the snake's metabolism prior to eating. The periods of observation in this March experiment and in the July experiment following were separated by intervals of varying length. In all the other digestion experiments with this python, however, the periods were continuous. The first

observation in the March experiment began 22 hours after food and lasted for 16 hours. The second observation began 50 hours after food and lasted 13 hours. When the periods of observation are so long and so far apart, they should, strictly speaking, be represented on the chart not by points but by blocks. Thus, it is highly probable that the peak effect of

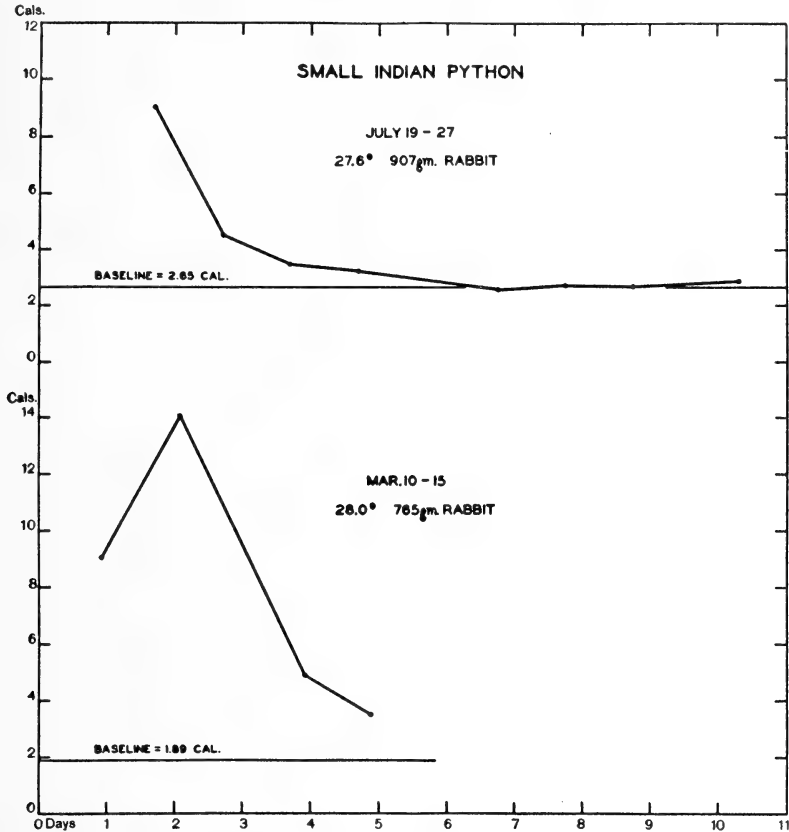


FIG. 69—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—SMALL INDIAN PYTHON.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake, are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

digestion or the increase in heat production to 14 calories which, as shown in figure 69, occurred 2 days and 2 hours after eating, is not far from that actually persisting over a considerable period of time rather than at one moment. The experiment was not continued long enough for the metabolism to return to the predigestive level, and yet the curve shows that it was rapidly approaching this level.

The peak effect of digestion can be influenced by the quantity of food ingested and by the level of the baseline, assuming that the temperature



of the environment remains the same. When the snake is emaciated and has a small body weight and a low metabolism, the increase in metabolism following food ingestion may be very great, expressed percentagewise. This is strikingly brought out with the small Indian python in the digestion experiment of March 10 to 15, when the maximum increase in heat production above the baseline was over 600 per cent. The snake had been fasting 128 days when the baseline value was determined. The interesting problem as to whether the same weight of food at the same environmental temperature would produce the same effect whether the animal had been fasting 14 days or 14 months can not be answered. In the latter case the body weight would be at a much lower level, and the

TABLE 61—*Metabolism of small Indian python during protein digestion*  
(27.6° C.; 907-gm. rabbit eaten July 17)

Date	Body weight	Time since eating		Length of period	Per kg. per 24 hours	
					Carbon dioxide	Heat produced
1916	kg.	days	hrs.	hrs.	gm.	cal.
May 13, 19, 20	6.54	69	.....	.....	0.795	2.65
July 19-20	6.93	1	17	20	2.826	9.00
July 20-21	6.90	2	17	20	1.398	4.45
July 21-22	6.87	3	17	20	1.098	3.49
July 22-23	6.85	4	16	21	1.006	3.20
July 24-25	6.71	6	18	20	.811	2.58
July 25-26	6.59	7	17	20	.862	2.74
July 26-27	6.47	8	17	20	.825	2.63
July 27	6.35	10	6	6	.886	2.82

rabbit or other food eaten would represent a larger proportion of the total weight at a much lower metabolic baseline. The possibility of studying the influence of digestion when, as a result of prolonged fasting, enormous changes in the body weight may be arbitrarily imposed should be considered.

A second digestion experiment (see table 61) was made with the small Indian python in July 1916, at an average temperature of 27.6° C. Standard values for comparison were obtained on May 13, 19 and 20 of the same year, at the same temperature level. The average standard carbon-dioxide production on these dates (0.795 gram) was much higher than that used for comparison with the data in the first digestion experiment, although the body weight was somewhat less. But the standard values in the first instance were obtained when the snake had been fasting 128 days, and in the second instance when it had been fasting only 69 days on the average. According to the general curve in figure 45 (p. 199) representing the course of the standard heat production of this snake during its short fasts, the metabolism at 27.6° C. would be 2.80 calories or, converted to carbon dioxide, 0.840 gram, a somewhat higher

value than the average for May 13, 19 and 20. Since the difference is only slight, the actually determined standard values in May should be used for comparison purposes. On July 17 the python ate a 907-gram rabbit, representing 15 per cent of its own body weight, or somewhat larger than that eaten in the March experiment. It had not previously been fed for 39 days. It was taken to the laboratory and put into the chamber on the afternoon of July 18. The environmental temperature was nearly the same in both experiments. The heat production during the first period of observation in the July experiment (1 day and 17 hours after food) increased to about the same height as that noted during the first period of the March experiment (22 hours after food). But thereafter the heat production immediately began to decrease, for the peak effect of digestion (a 240 per cent increase) was less in the July than in the March experiment. The charted curve for the July experiment (see the upper half of figure 69) shows much the same picture as that for the March experiment. The July observations were continued until the python's metabolism returned to the baseline of 2.65 calories.

#### PROTEIN DIGESTION AT 22° C.

It was clear from the July experiment that the observations should be made in shorter, more frequent periods in order to measure the carbon-dioxide production as soon as possible after the snake had eaten and to determine the characteristic course of the metabolism during the digestive cycle. In the following experiments with the small python, therefore, the periods were for the most part only from one or two to five or six hours long, were continuous, and in all but two instances the first period of the series began within one hour after food was eaten. The protein digestion experiment of November 6 to 14 was made at an average environmental temperature of 21.8° C. The standard value for comparison can be secured from two sources, from actually conducted fasting experiments prior to and at the same temperature as the digestion experiment and from the measured level which the metabolism seeks after digestion has ceased. In the July digestion experiment, the measured standard metabolism prior to the ingestion of food and the level to which the metabolism fell after the rabbit was eaten confirm each other. Immediately prior to the digestion experiment of November 6 to 14, namely, on October 28-29, five low values averaging 1.63 calories at 21.6° C. were found. This average is not far from the two values secured previously on April 8-9 and April 18-19, averaging 1.77 calories at 21.9° C. On October 20 to 23, three values secured at the average temperature of 23.2° C. averaged 2.02 calories, which, when reduced 10 per cent (as outlined on page 251) to correct it approximately to a temperature of 21.8°, amounts to 1.82 calories. Although these standard values do not agree closely,<sup>1</sup> they con-

<sup>1</sup> The discordance in the various baselines ascribed to the different experiments plays little, if any, rôle in the specific measurement under discussion in this section, namely, the *increase* in metabolism following food. Taken by themselves, the different baselines give a disconcerting indication of the irregularity in the measured standard metabolism of the snake, particularly at the lower temperatures. It has already been noted on pages 198 to 201 that the length of fast and the nutritive state of the animal are important factors in determining the standard metabolism.

TABLE 62—*Metabolism of small Indian python during protein digestion*  
(21.8° C.; 454-gm. rabbit eaten Nov. 5)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1916 Oct. 28-29	<i>days hrs.</i> 103	.....	<i>gm.</i> 0.489	<i>cal.</i> 1.63
Nov. 6	17	1	1.195	3.80
	20	2	1.161	3.70
	23	3	.981	3.12
	1 2	4	1.063	3.38
Nov. 6-7	1 5	5	1.182	3.76
Nov. 7	1 8	6	1.110	3.53
	1 11	7	1.131	3.60
	1 13	8	1.234	3.93
	1 16	9	1.173	3.73
	1 18	10	1.251	3.98
	1 21	11	1.293	4.12
	2 1	12	1.600	5.09
Nov. 7-8	2 3	13	1.595	5.08
Nov. 8	2 7	14	1.762	5.61
	2 9	15	1.610	5.12
	2 13	16	1.512	4.81
	2 16	17	1.668	5.31
	2 19	18	1.726	5.49
	2 21	19	1.727	5.50
	2 23	20	1.741	5.54
	3 1	21	1.596	5.08
Nov. 8-9	3 3	22	1.546	4.92
Nov. 9	3 6	23	1.850	5.89
	3 8	24	1.830	5.82
	3 10	25	1.681	5.35
	3 12	26	1.446	4.60
	3 14	27	1.502	4.78
	3 16	28	1.536	4.89
	3 18	29	1.430	4.55
	3 20	30	1.458	4.64
	3 22	31	1.360	4.33
	4 0	32	1.212	3.86
Nov. 9-10	4 3	33	1.068	3.40
Nov. 10	4 7	34	1.100	3.50
	4 10	35	1.298	4.13
	4 13	36	1.279	4.07
	4 16	37	1.130	3.60
	4 19	38	1.022	3.25
	4 22	39	1.000	3.18
Nov. 10-11	5 3	40	.906	2.88
Nov. 11	5 9	41	.868	2.76
	5 15	42	.856	2.72
	5 21	43	.759	2.42
Nov. 11-12	6 3	44	.744	2.37
Nov. 12	6 10	45	1.028	3.27
	6 17	46	.909	2.89
Nov. 12-13	6 23	47	.674	2.45
Nov. 13	7 6	48	.815	2.59
	7 13	49	.811	2.58
	7 20	50	.812	2.58
	7 22	51	.775	2.47
Nov. 13-14	8 0	52	.771	2.45
Nov. 14	8 7	53	.751	2.39
	8 13	54	.778	2.48

<sup>1</sup> Snake weighed 5.89 kg. on Oct. 28-29, 6.16 kg. on Nov. 6, and 6.02 kg. on Nov. 14 after it was removed from the respiration chamber. Weight assumed to have decreased to 6.04 kg. in periods 49 to 54.

firm each other to a certain extent, and it therefore seems best to use for comparison purposes the results of the observations on October 28-29, namely, 0.489 gram of carbon dioxide or 1.63 calories. At this time the

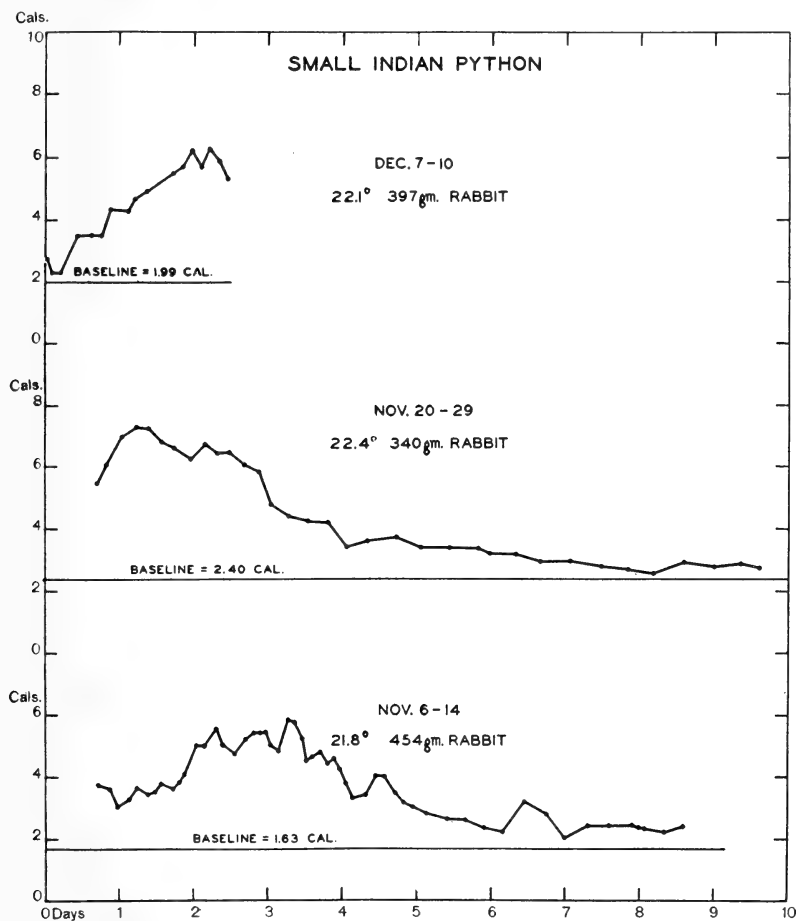


FIG. 70—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—SMALL INDIAN PYTHON.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake, are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

python had been fasting 103 days or nearly the same length of time as at the beginning of the digestion experiment on November 6.

On November 5 the python ate a 454-gram rabbit equivalent to 8 per cent of its own weight. It had not been fed previously since the night of July 17-18 or for 3 months and 19 days. It was put into the respiration chamber at about 10 a.m., November 6, and the first period began at 11<sup>h</sup>45<sup>m</sup> a.m., or 17 hours after food. The carbon-dioxide production was

then measured in 54 continuous periods, each from 2 to 7 hours long, extending from November 6 to November 14. As can be seen from table 62, the carbon-dioxide production 17 hours after food was more than double the standard value. It reached its highest point 3 days and 6 hours after food, namely at 1.850 grams. Thereafter there was an almost continuous fall until in the fifty-fourth period on November 14 a value of 0.778 gram was reached, which was nearly 60 per cent above the standard value used for comparison. It is debatable whether the standard metabolism of the python at this time is not best expressed by the last few values obtained on November 13 and 14 rather than by those obtained on October 28-29.

The course of the metabolism following the ingestion of food in this experiment of November 6 to 14 is shown graphically by the lowest curve in figure 70. The peak effect of digestion (261 per cent increase in heat production) was somewhat greater in this experiment than in the preceding experiment. The time for return to the baseline was slower, for although the heat production had reached a fairly constant level at about the sixth or the seventh day after food, it was still higher than the baseline. The environmental temperature, however, was about 6 degrees lower than that in the preceding July and March experiments and a smaller rabbit was eaten.

On November 19 the small python ate a 340-gram rabbit amounting to 6 per cent of its own body weight. It was put into the respiration chamber at 9<sup>h</sup>30<sup>m</sup> a.m., November 20, and the first period of observation began at 10<sup>h</sup>55<sup>m</sup> a.m. The experiment continued for 34 periods without interruption and ended on November 29 (table 63). The python had also been fed 14 days previous, on November 5, but since the stimulus to metabolism resulting from the food had, in accordance with the curve for the digestion experiment of November 6 to 14, practically disappeared at the end of 6 or 7 days, it is reasonable to assume that the python's metabolism had reached the standard level by November 19. The digestion experiment of November 20 to 29 was carried out at an average temperature of 22.4° C., a temperature but 0.6° higher than that of November 6 to 14. Consequently one could assume that the baseline for comparison with the second November experiment would be the same as that used for comparison with the first November experiment, namely, 1.63 calories, or one could use as the baseline the level of the metabolism at the end of the digestion experiment of November 6 to 14, approximately 2.40 calories. (See lowest curve in figure 70.) According to the curve for the *short* fasts of the small python (fig. 45) the standard heat production at 22.4° C. would be 1.88 calories or materially lower. On the other hand, two months later, on January 24 to 26, the standard metabolism was 2.41 calories at 22.8° C. In order to determine the total increment in heat production due to the ingestion of a definite amount of food, it is of importance to know the absolute level of the standard metabolism at the start of the digestion experiment. But for the immediate purpose in hand, that is, to note the rapidity and intensity of the rise in metabolism following food ingestion, it is relatively unimportant whether the standard metabolism is 2.40 or 2.60 calories. The best procedure would have been

to have conducted an experiment to determine the standard metabolism immediately preceding the digestion experiment itself. Since this was not done, the most logical standard value to use is that found about

TABLE 63—*Metabolism of small Indian python during protein digestion*  
(22.4° C.; 340-gm. rabbit eaten Nov. 19)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
	days hrs.		gm.	cal.
1916 Nov. 14	8 14	.....	.....	2.40
Nov. 20	17	1	1.726	5.49
	20	2	1.929	6.14
	1 0	3	2.212	7.04
Nov. 20-21	1 5	4	2.312	7.36
Nov. 21	1 9	5	2.283	7.27
	1 13	6	2.158	6.87
	1 17	7	2.100	6.68
	1 22	8	1.994	6.35
Nov. 21-22	2 3	9	2.135	6.80
Nov. 22	2 7	10	2.054	6.54
	2 11	11	2.059	6.55
	2 16	12	1.931	6.15
	2 20	13	1.864	5.93
Nov. 22-23	3 0	14	1.525	4.85
Nov. 23	3 6	15	1.417	4.51
	3 12	16	1.375	4.38
	3 18	17	1.347	4.29
Nov. 23-24	4 0	18	1.108	3.53
Nov. 24	4 7	19	1.166	3.71
	4 16	20	1.193	3.80
Nov. 24-25	5 0	21	1.105	3.52
Nov. 25	5 10	22	1.112	3.54
	5 19	23	1.092	3.48
Nov. 25-26	5 22	24	1.062	3.38
Nov. 26	6 7	25	1.036	3.30
	6 15	26	.972	3.09
Nov. 26-27	7 0	27	.988	3.14
Nov. 27	7 10	28	.933	2.97
	7 19	29	.882	2.81
Nov. 27-28	8 3	30	.858	2.73
Nov. 28	8 13	31	.963	3.07
Nov. 28-29	8 22	32	.937	2.98
Nov. 29	9 7	33	.953	3.03
	9 13	34	.907	2.89

<sup>1</sup> Snake weighed 6.02 kg. on Nov. 14, 6.36 kg. on Nov. 20, and 6.25 kg. on Nov. 29 after it was removed from the respiration chamber. Weight assumed to have decreased to 6.26 kg. in periods 32 to 34.

November 14, only 5 days before, namely, 2.40 calories. Hence in figure 70 (p. 257), in which the data for this second November digestion experiment have been charted, a straight line has been drawn indicating the baseline as 2.40 calories. This baseline is confirmed to a certain extent by the fact that at the end of this experiment the metabolism has returned to nearly this level, although it is a little higher.

These two November experiments were made at nearly the same temperature. The rabbit eaten in the first experiment (454 grams) was somewhat larger than that eaten in the second experiment (340 grams). The peak effect of digestion was reached in the first November experiment 3 days and 6 hours after food; in the second November experiment shortly after the first day. The maximum increase in heat production was 207 per cent in the second series as compared with 261 per cent in the first.

TABLE 64—*Metabolism of small Indian python during protein digestion*  
(22.1° C.; 397-gm. rabbit eaten Dec. 7)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1916 Dec. 6-7	<i>days hrs.</i> 17	.....	<i>gm.</i> 0.597	<i>cal.</i> 1.99
Dec. 7	1	1	.877	2.79
	2	2	.713	2.27
Dec. 7-8	5	3	.735	2.34
Dec. 8	10	4	1.110	3.53
	15	5	1.092	3.48
	18	6	1.119	3.56
	21	7	1.377	4.38
	1 2	8	1.345	4.28
Dec. 8-9	1 5	9	1.462	4.65
Dec. 9	1 8	10	1.550	4.93
	1 16	11	1.736	5.53
	1 20	12	1.812	5.77
	1 23	13	1.950	6.21
	2 2	14	1.793	5.71
Dec. 9-10	2 5	15	1.963	6.25
Dec. 10	2 8	16	1.838	5.85
	2 10	17	1.673	5.33

<sup>1</sup> Snake weighed 6 kg. on Dec. 6-7 and 6.40 kg. on Dec. 7. Assumed to have weighed 6.40 kg. throughout the entire digestion experiment.

The general trend of the metabolism following the maximum increase is much the same in both experiments, but the final level to which it falls is slightly higher in the second experiment.

On November 20 it was believed that the python would probably shed in about a week. It had started to shed when taken to the reptile house on November 29 and had not quite finished on December 4.

On December 7 to 10 another digestion experiment (table 64) was made at an average temperature of 22.1° C. The python ate a 397-gram rabbit on December 7, equivalent to 7 per cent of its own weight. It had not been fed previously since November 19 or for 18 days. In this particular instance a fasting experiment at the same temperature was carried out prior to the digestion experiment, to determine the standard metabolism before the animal was fed. The snake remained inside the respiration chamber

following the fasting experiment, which ended at 1<sup>h</sup>27<sup>m</sup> p.m., December 7, and the rabbit was placed inside the chamber with it at 2<sup>h</sup>30<sup>m</sup> p.m. and there eaten. The first period of the digestion experiment began at 4<sup>h</sup>40<sup>m</sup> p.m., or 45 minutes after the rabbit was eaten. The python was much agitated as a result of the feeding process, but was quiet during the experiment itself, except for a few slight movements. The standard metabolism in the fasting experiment of December 6-7 at 22.0° C. was 1.99 calories. According to the curve for the short fasts of this snake the standard value at this temperature would be 1.80 calories, but the actually determined value of 1.99 calories was used for comparison. Immediately after feeding, as will be seen in table 64 and in the uppermost curve in figure 70 (p. 257), the heat production began to rise and the maximum increase (214 per cent) was reached in about 2 days. The experiment had to be terminated on December 10, but at this time there was every indication that the metabolism had begun to decrease. The important features of this experiment are that the standard metabolism was measured immediately prior to the digestion period and observations were made during the first few hours of digestion, which were missing in the preceding experiments.

#### PROTEIN DIGESTION AT 17° C.

Knowing the pronounced influence of a low environmental temperature in depressing the standard metabolism of this python, we wished to note how the digestive cycle would be altered by a low temperature. A protein digestion experiment was therefore made on January 2 to 18 at an average temperature of 17.6° C. (table 65). The python had been placed in the respiration chamber on December 29 at a temperature of 25° C. On January 1 the temperature was changed to about 17° C. The rectal temperature of the python at 2 p.m., January 2, was 17.6° C. At this time the python was given a 454-gram rabbit, equivalent to 8 per cent of its weight. The snake struck the rabbit while it was being put into its cage but did not swallow it until 5 p.m. The first experimental period began at 6 p.m. the same day. The snake had presumably not been fed since December 7, or for 26 days. The standard metabolism was not measured immediately before this experiment, and we have recourse only to the results obtained in fasting experiments on October 30 to November 4, 1916, and on January 31 to February 3, 1917. In the first of these two fasting series, the standard metabolism at 16.6° C. averaged 0.91 calorie. According to the curve in figure 45 (p. 199), representing the short fasts of this python, the metabolism between 20° and 30° increases 16 per cent with each degree increase in temperature. The heat production of 0.91 calorie at 16.6° C., therefore, if corrected to 17.6° C. (the temperature of the January digestion experiment) would be 1.06 calories. In the second of the two fasting experiments the standard heat production was 1.10 calories at 17.4° C. According to the curve for the short fasts the standard metabolism would be 1.05 calories at 17.6° C. A round figure of 1.00 calorie may therefore justifiably be used as the baseline for this January digestion experiment. Undoubtedly the first period of this digestion experiment was complicated by the fact that the python was much



TABLE 65—*Metabolism of small Indian python during protein digestion*  
(17.6° C.; 454-gm. rabbit eaten Jan. 2)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	days hrs.		gm. %0.300	cal. %1.00
.....	.....	.....		
Jan. 2	1	1	.698	2.22
Jan. 2-3	4	2	.452	1.44
Jan. 3	11	3	.396	1.26
	17	4	.459	1.46
Jan. 3-4	23	5	.474	1.51
Jan. 4	1 7	6	.492	1.57
	1 14	7	.376	1.20
	1 21	8	.508	1.62
Jan. 4-5	2 4	9	.442	1.41
Jan. 5	2 11	10	.447	1.42
	2 17	11	.662	2.11
Jan. 5-6	3 0	12	.516	1.64
Jan. 6	3 8	13	.633	2.01
	3 14	14	.517	1.65
Jan. 8	5 19	1	1.874	5.96
	5 22	2	1.397	4.45
Jan. 8-9	6 5	3	.972	3.09
Jan. 9	6 11	4	.751	2.39
	6 18	5	.730	2.32
Jan. 9-10	7 4	6	.672	2.14
Jan. 10	7 13	7	.703	2.24
	7 21	8	.700	2.23
Jan. 10-11	8 5	9	.700	2.23
Jan. 11	8 14	10	.645	2.05
	8 23	11	.611	1.94
Jan. 11-12	9 5	12	.615	1.96
Jan. 12	9 14	13	.659	2.10
	9 22	14	.657	2.09
Jan. 12-13	10 4	15	.600	1.91
Jan. 13	10 15	16	.629	2.00
Jan. 13-14	11 1	17	.630	2.01
Jan. 14	11 12	18	.572	1.82
Jan. 14-15	12 0	19	.666	2.12
Jan. 15	12 12	20	.643	2.05
Jan. 15-16	12 22	21	.610	1.94
Jan. 16	13 9	22	.630	2.01
Jan. 16-17	13 21	23	.591	1.88
Jan. 17	14 9	24	.628	2.00
Jan. 17-18	14 21	25	.603	1.92
Jan. 18	15 10	26	.625	1.99

<sup>1</sup>Snake weighed 6.36 kg. on Jan. 2 and was assumed to have weighed this through Jan. 6. It weighed 6.18 kg. on Jan. 8, and 6.12 kg. on Jan. 18 after it was removed from respiration chamber. Weight assumed to have decreased to 6.12 kg. in periods 25 and 26.

<sup>2</sup>See explanation regarding this baseline value on page 261.

<sup>3</sup>A 454-gram rabbit (body temp. 40° C.) cooled to temperature of snake (17.6°) would yield about 10 calories. Effect of this heat not considered here or in other experiments.

agitated as a result of eating. The carbon-dioxide production is therefore high, 0.698 gram, at the start but falls off during the next two periods and then has a tendency to remain constant for the rest of the experiment through January 6.

It was feared that the prolonged digestion at the low temperature might prove harmful to the snake, and on January 6 the python was taken to the reptile house and placed in a warm environment. The rectal temperature at the close of the observations on January 6, before the snake was taken to the reptile house, was  $17.9^{\circ}\text{C}$ ., when the environmental temperature was  $17.6^{\circ}\text{C}$ . Although this body temperature was obtained only  $3\frac{1}{2}$  days after food, it is probable that there was not a considerable amount of digestive activity going on, because of the low environmental temperature. On January 8 the rectal temperature was  $30.7^{\circ}\text{C}$ ., when the gravel of the cage was  $28.4^{\circ}\text{C}$ . The python was brought from the reptile house to the laboratory through the cold air outdoors and put

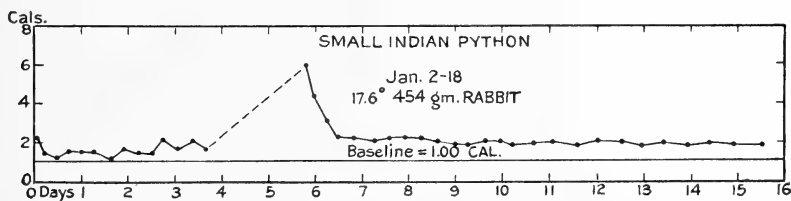


FIG. 71—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—SMALL INDIAN PYTHON.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake, are indicated on chart near curve. *Standard* heat production per kilogram of body weight per 24 hours at same environmental temperature as that of digestion experiment is shown by "baseline" below curve. That portion of curve represented by a broken line indicates time when python was removed from respiration chamber.

into the respiration chamber at about  $17^{\circ}\text{C}$ . The observations were continued from January 8 until January 18. From table 65 it can be seen that the carbon-dioxide production was high for the first three periods following the snake's return to the respiration chamber, probably due in large part to the agitation caused by the transportation and likewise to the fact that the rectal temperature had been as high as  $30.7^{\circ}\text{C}$ . before the measurements began, although it must have fallen considerably by the end of the third period. By the fourth period on January 9 the metabolism had reached nearly the same level that it had attained about the third day after food and remained at this level without material alteration until January 18, when the python was again taken to the reptile house for a few days to finish digestion in a warmer environment.

The results of this January digestion experiment are plotted in figure 71. It can be seen that the heat production averaged about 1.8 calories until the python was removed to the reptile house about the middle of the fourth day (indicated by the broken line in the curve in figure 71). On its return to the respiration chamber the metabolism was high, occasioned, as explained above, by agitation and its high rectal temperature.

The metabolism rapidly decreased and after the middle of the seventh day remained at a level of about 2 calories as long as the experiment continued. This level is 100 per cent above the baseline, which has been

TABLE 66—*Metabolism of small Indian python during protein digestion*  
(28.4° C.; 425-gm. rabbit eaten Feb. 5)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	<i>days hrs.</i>		<i>gm.</i>	<i>cal.</i>
Jan. 29-30	27	.....	<sup>2</sup> 1.22	<sup>2</sup> 4.07
Feb. 5	1	1	1.432	4.56
	4	2	2.000	6.37
	6	3	2.305	7.34
Feb. 5-6	8	4	2.559	8.15
Feb. 6	10	5	2.819	8.97
	11	6	3.111	9.90
	12	7	3.356	10.68
	14	8	3.755	11.95
	15	9	4.044	12.87
	16	10	4.376	13.93
	19	11	4.688	14.92
	20	12	4.542	14.46
	21	13	4.536	14.44
	23	14	4.730	15.06
	1	15	4.466	14.22
	1	16	3.984	12.68
	1	17	4.388	13.97
Feb. 6-7	1	18	2.844	9.05
Feb. 7	1	19	3.952	12.58
	1	20	3.383	10.77
	1	21	3.094	9.85
	1	22	2.511	7.99
	1	23	2.264	7.21
	2	24	2.212	7.04
	2	25	2.364	7.52
Feb. 7-8	2	26	2.135	6.80
Feb. 8	2	27	2.034	6.47
	2	28	2.076	6.61
	2	29	1.862	5.93
	3	30	1.671	5.32
Feb. 8-9	3	31	1.568	4.99
Feb. 9	3	32	1.697	5.40
	3	33	1.563	4.98
	4	34	.....	.....
Feb. 9-10	4	35	1.393	4.43
Feb. 10	4	36	1.601	5.10
	4	37	1.672	5.32

<sup>1</sup> Snake weighed 5.85 kg. on Jan. 29-30, 6.19 kg. on Feb. 5, and 6.12 kg. on Feb. 10 after it was removed from respiration chamber. Weight assumed to have decreased to 6.15 kg. in periods 34 to 37.

<sup>2</sup> Corrected to 28.4° C.; see page 265.

considered to be 1.00 calorie. It is clear that the digestion was by no means completed even at the end of 15 or 16 days, although the digestion had been aided by a stay of nearly two days at a higher temperature in the reptile house. This is a striking illustration of the slowness in digestion at the low temperature of 17° C.

## PROTEIN DIGESTION AT 28° AND 37° C.

The apprehension that some damage might be done to the python by subjecting it to a low temperature during the digestive cycle precluded using it for further observations at 17° C., and the final studies of digestion with this snake were made at higher temperatures, the last one at a higher temperature than any employed previously. On February 5 the python ate a 425-gram rabbit, representing 7 per cent of its weight. It had not eaten previously since January 2 or for 1 month and 3 days. It was placed in the respiration chamber 3 hours before being fed, and the

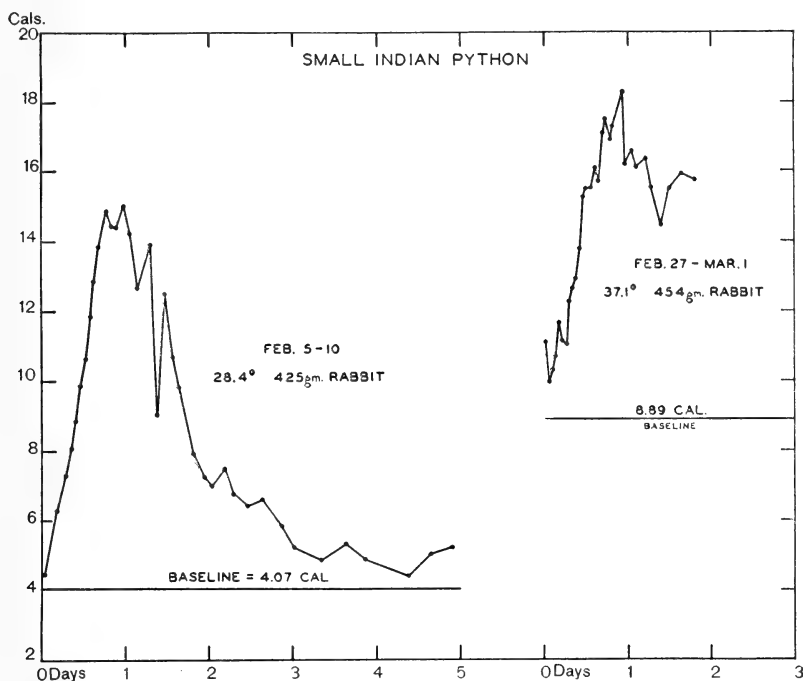


FIG. 72—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—SMALL INDIAN PYTHON.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake, are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

rabbit was given to it there. Shortly after devouring the rabbit, the python became quiet and the experiment could begin. Observations during digestion were made from February 5 to 10 at an average temperature of 28.4° C. Standard metabolism measurements were made on January 29-30 at a temperature of 29.6° C. Corrected for the higher temperature, on the assumption that each degree decrease between 30° and 20° C. causes a 6 per cent decrease in metabolism (according to the curve for the short fasts of this python in figure 45, page 199), the standard heat production at 28.4° C. would be 4.07 calories (1.22 grams of carbon dioxide), but ac-

according to the curve for the short fasts it would be only 3.0 calories. It seems more logical, however, to use for comparison the standard value determined on January 29-30, only a few days prior to the digestion ex-

TABLE 67—*Metabolism of small Indian python during protein digestion*  
(37.1° C.; 454-gm. rabbit eaten Feb. 27)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	<i>days hrs.</i>		<i>gm.</i>	<i>cal.</i>
Feb. 27	22	.....	2.669	8.89
Feb. 27	5 mins.	1	3.477	11.07
	1	2	3.140	9.99
	2	3	3.252	10.35
	3	4	3.364	10.71
	4	5	3.664	11.66
	5	6	3.514	11.19
	6	7	3.477	11.07
Feb. 27-28	7	8	3.850	12.25
Feb. 28	8	9	3.963	12.61
	9	10	4.075	12.97
	10	11	4.336	13.80
	11	12	4.785	15.23
	12	13	4.860	15.47
	13	14	4.870	15.50
	14	15	5.054	16.09
	15	16	4.935	15.71
	16	17	5.383	17.13
	17	18	5.495	17.49
	18	19	5.308	16.90
	19	20	5.421	17.26
	20	21	<sup>2</sup> 6.942	<sup>2</sup> 22.10
	22	22	5.727	18.23
	23	23	5.091	16.20
	1	1	5.214	16.60
	1	2	5.054	16.09
	1	4	5.149	16.39
Feb. 28-Mar. 1	1	6	4.887	15.56
Mar. 1	1	9	4.540	14.45
	1	11	4.881	15.54
	1	15	5.011	15.95
	1	16	<sup>2</sup> 5.599	<sup>2</sup> 17.82
	1	18	4.957	15.78

<sup>1</sup> Snake weighed 5.95 kg. on Feb. 27, before eating, and 6.42 kg. after eating. Weight assumed to be 6.37 kg. in periods 22 to 32. Weighed 6.32 kg. sometime after removal from respiration chamber.

<sup>2</sup> Snake active. Result not plotted in figure 72.

periment itself. As will be seen from table 66, the carbon-dioxide production began to increase during the first few hours after food, and the increase continued until the maximum was reached about the twenty-third hour. Thereafter the carbon-dioxide production gradually fell off and the last observation on February 10 showed a production of 1.672 grams. The details of the experiment of February 5 to 10 are charted in

figure 72. The increase in heat production (270 per cent above the baseline) during the first day is strikingly shown. The baseline of 4.07 calories had not been reached even toward the end of the fifth day after food, when the experiment terminated.

In the last digestion experiment with the small Indian python, on February 27 to March 1, at the high temperature of 37° C., fortunately the baseline was determined immediately preceding the digestive cycle. In five 3-hour periods on February 27 when the python had been 22 days without food, the standard heat production was found to be 8.89 calories at an average temperature of 37.9° C. and the carbon-dioxide production 2.669 grams. At 3<sup>h</sup>05<sup>m</sup> p.m. on February 27 a 454-gram rabbit was given to the python, which had not eaten since February 5, or for 22 days. The rabbit, which represented 8 per cent of the snake's weight, was not swallowed until about 4 p.m., and the first period of measurement began at 4<sup>h</sup>05<sup>m</sup> p.m. There was apparently but little activity immediately after feeding. The carbon-dioxide production increased enormously as a result of the food (table 67). The maximum production, 6.942 grams, occurred at the twentieth hour. The striking difference between the values for the twentieth and the twenty-second periods and the twenty-first period led to an examination of the protocols, which show clearly that the snake was pronouncedly active during the twenty-first period. Hence in this period the metabolism was affected not only by the digestion but by activity. Consequently in plotting the data for this experiment (fig. 72, p. 265) we have purposely omitted this period. Similarly, in period 31 the metabolism was affected by activity and this period does not appear on the chart. The values for these two periods have an interest of themselves, however, since they show that it is possible for an ordinarily quiet snake to increase its metabolism from 12 to 28 per cent by activity. The metabolism had not returned to the baseline at the end of 1 day and 18 hours, when the experiment terminated, but the belief that snakes do not withstand high temperatures well and the monetary value of this python made it undesirable to continue the experiment longer. The maximum increase in heat production above the baseline, not including the active periods, was 105 per cent.

#### CONCLUSIONS REGARDING INFLUENCE OF PROTEIN INGESTION ON METABOLISM OF THE PYTHON

The striking features of the protein experiments with the small python are that at the low temperature the increase in metabolism following protein ingestion is relatively small but continues over a long period; at the intermediate temperatures the increase is marked but there is a fairly rapid return to the baseline; and at the high temperatures the ingestion of protein has an almost explosive effect, resulting in a high peak in the production of heat and a fall thereafter.

At 17.6° C. the heat production was increased from a baseline of 1.00 calorie to about 2 calories, an increase of 100 per cent. This increase persisted for a period of at least 16 days. How much longer it would have lasted is not known, since the experiment was not continued beyond

this time. At the intermediate temperature of  $22^{\circ}$  C. the smoothed curve in figure 73 indicating the general course of the heat production following the ingestion of protein during three digestive cycles shows that the peak in the heat production above the average baseline of 2 calories was not far from 6 calories, that is, the metabolism was increased on the average 200 per cent. In the February experiment at  $28.4^{\circ}$  C. the baseline was 4.07 calories and the heat production rose to a peak of 15.06 calories, an increase of 270 per cent. At  $37^{\circ}$  C. the baseline was 8.89 calories and the heat production rose to 18.23 calories or was increased 105 per cent. Since exactly the same amount of protein was not given to the python in each experiment, the percentage increases in metabolism can not be compared directly. It is probably illogical to compare the increases computed

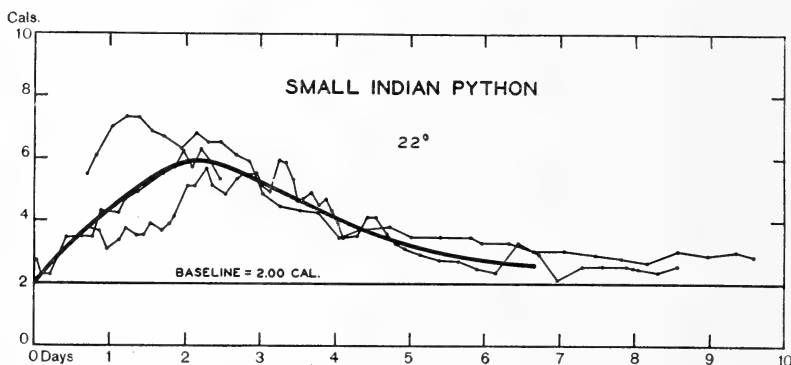


FIG. 73—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS (AT  $22^{\circ}$ ) REFERRED TO DAYS AFTER PROTEIN INGESTION—SMALL INDIAN PYTHON.

Heavy, smoothed curve represents average trend of metabolism during protein digestion at  $22^{\circ}$  C. Lighter weight curves are reproductions of curves shown in figure 70. *Standard* heat production per kilogram of body weight per 24 hours, at  $22^{\circ}$  C., is indicated by "baseline" below curves.

per 500 grams of rabbit. We had hoped to be able to feed the snake a 500-gram rabbit and note the increase in metabolism throughout the entire digestive cycle, to determine how much the excess heat production resulting from the ingestion of a definite amount of protein would vary at the different environmental temperatures. According to the calculations just given, the maximum increase (an increase which with humans is frequently spoken of as the "specific dynamic action of food") was 200 and 270 per cent at  $22^{\circ}$  and  $28^{\circ}$  C., and only 100 and 105 per cent at  $17^{\circ}$  and  $37^{\circ}$  C., respectively. The variability in this percentage increase was in large part due to the shifting baselines as a result of the different temperatures at which the experiments were made and possibly to different baselines representing different nutritive states incidental to longer or shorter fasts.

The general nature of the curves shows the length of time required for digestion. Thus, at  $17.6^{\circ}$  the digestion was still continuing at the end of the fifteenth day, with no certainty of returning to the baseline. At a higher temperature,  $22^{\circ}$ , the curve in figure 73 suggests that the baseline was

reached approximately on the seventh day. At 28° the baseline was nearly reached on the fourth or fifth day. The high temperature of 37° prevented our continuing the experiment sufficiently long, but all the indications were that there is a rapid digestion at this temperature compared with the digestion at 22° and 17°. The rate of protein digestion was therefore approximately dependent upon the temperature level, being slower at the low temperatures than at the higher temperatures.

#### Boa B

The first protein digestion experiment with a boa was with boa B in April 1916, and like our first experiment with the python, consisted of observations of from 4 to 8 hours on successive days rather than continuous periods of observation. The results are shown in table 68 and figure 74.

TABLE 68—*Metabolism of boa B during protein digestion*  
(28.1° C.; 397-gm. pigeon eaten April 8)

Date	Body weight	Time since eating	Length of period	Per kg. per 24 hours	
				Carbon dioxide	Heat produced
1916	kg.	days hrs.	hrs.	gm. 10.645	cal. 12.15
Apr. 9	12.59	13	4	.991	3.15
Apr. 10	12.56	1 12	6	1.282	4.08
Apr. 11	12.53	2 12	6	1.669	5.31
Apr. 12	12.53	3 11	8	1.635	5.20
Apr. 13	12.16	4 13	5	1.385	4.41
Apr. 14	12.10	5 11	7	1.102	3.51
Apr. 15	12.07	6 11	7	1.190	3.79
Apr. 17	11.87	8 11	6	1.020	3.40
Apr. 19	11.82	10 11	6	.950	3.17
Apr. 20	11.77	11 11	6	1.088	3.63

<sup>1</sup> Based on curve in figure 54, page 224.

At midnight, April 8, boa B ate a 397-gram pigeon, equivalent to 3 per cent of its weight. It had not eaten previously for nearly two months. The digestion experiment began on April 9 and intermittent observations were made through April 20, twelve days after the food was eaten. The average environmental temperature was 28.1° C. Excreta were found in the snake's box before the experiment of April 13. The amount removed April 18 was 255 grams, and the body weights of April 13, 14 and 15 were corrected for the same.

Three standard metabolism experiments were made with boa B on April 5, 6 and 7 at about the same temperature as the digestion experiment. But there was such a disagreement in the results (table 31, p. 160) that it seems better to assume as a baseline for comparison with the digestion experiment the average standard metabolism at 28° C. as shown by the general smoothed curve for all boas in figure 54 (p. 224), namely, 0.645 gram of carbon dioxide and 2.15 calories. The baseline values have been



underlined in table 68. After the pigeon was eaten, the snake's carbon-dioxide production increased steadily during the first three periods of the experiment. The production during the fourth period was practically

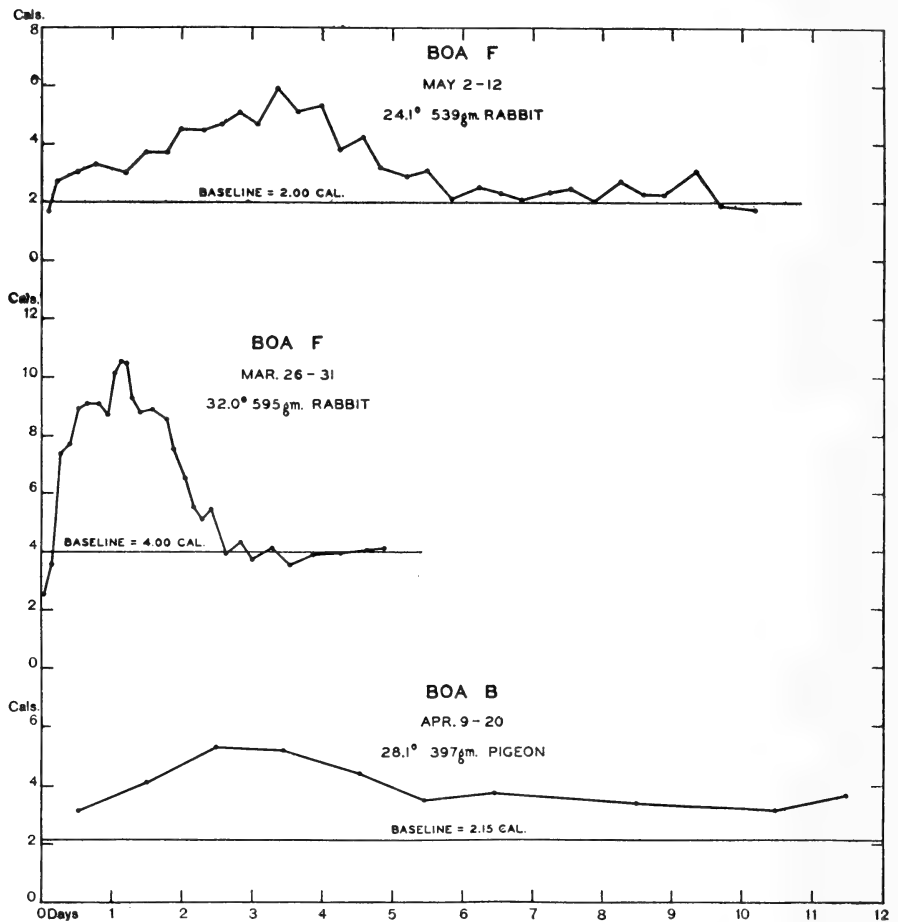


FIG. 74—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—BOAS B AND F.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake, are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

the same as that during the third. It then began to fall off, although at the end of 6 days and 11 hours it was still 85 per cent above the pre-digestive level. On April 17, 19 and 20 the metabolism had reached a reasonably constant level, but seemingly had not returned to the assumed baseline. The maximum increase in heat production above the baseline was 147 per cent.

## Boa F

With boa F three digestion experiments were made, the results of which are reported in tables 69, 70 and 71. In the first experiment on March 15 to 17 food had been put into the snake's cage on March 13 and was probably eaten, although there was no visible lump in the middle of the snake. The amount and kind of food are not known. It has been assumed, in estimating the time since eating in this experiment, that the snake ate at 5 p.m., March 13, as that was the regular time for feeding the snakes at the Park. Boa F arrived at the Park on March 8, 1917, and other than the food of March 13 it may have been without food since it was captured. The environmental temperature during the digestion period was low, averaging 16.5° C. No baseline was established at this temperature, and hence one can only assume from the curve for all boas (fig. 54, p. 224)

TABLE 69—*Metabolism of boa F during protein digestion*  
(16.5° C.; probably ate on March 13)

Date	Body weight	Time since eating	Period	Per kg. per 24 hours	
				Carbon dioxide	Heat produced
1917	kg.	days hrs.	..	gm. 0.165	cal. 0.55
.....	.....	.. ..	..		
Mar. 15	5.98	1 18	1	.522	1.66
Mar. 15-16	(5.97)	1 21	2	.486	1.55
Mar. 16	(5.97)	2 8	3	.514	1.64
Mar. 16-17	(5.96)	2 21	4	.510	1.62
Mar. 17	(5.96)	3 12	5	.633	2.01

<sup>1</sup> Based on curve in figure 54, page 224.

that at 16.5° C. the standard heat production would probably be 0.55 calorie and the standard carbon-dioxide production 0.165 gram. One day and 18 hours after the snake ate, its carbon-dioxide production was 0.522 gram and remained at about this level until the last observation on March 17, when it increased to 0.633 gram (table 69). The heat production of 1.66 calories in the first period is 202 per cent above the assumed baseline. Under reasonably constant conditions at a temperature of 17.6° C. the python's metabolism (see page 267) increased above the probable baseline only 100 per cent. Unquestionably the digestion was still in progress when this experiment with boa F ended. On March 17, since it was realized that the digestive processes would be slow at this low temperature, boa F was taken to the reptile house and placed in a warm den with other snakes. There it probably had a rectal temperature of not far from 30° C. until it was brought back to the laboratory, but no standard metabolism measurements were made.

On March 25-26 boa F remained overnight at a temperature of about 24° or 25° C., to prepare it for a digestion experiment at 32°. The boa was in the respiration chamber at least 45 minutes before period 1. On

March 26 boa F ate a 595-gram rabbit, equivalent to 11 per cent of its weight, and the first observation in the respiration chamber began one hour after it had eaten. As in the first digestion experiment, the periods of observation were continuous and extended through March 31. The average environmental temperature was 32° C. The baseline at this tem-

TABLE 70—*Metabolism of boa F during protein digestion*

(32.0° C.; 595-gm. rabbit eaten March 26)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	days hrs.		gm.	cal.
.....	.....	..	<sup>2</sup> 1.062	<sup>2</sup> 3.54
Mar. 26	1	1	.777	2.47
	4	2	1.128	3.59
	7	3	2.321	7.39
Mar. 26-27	10	4	2.390	7.61
Mar. 27	13	5	2.785	8.86
	16	6	2.837	9.03
	20	7	2.837	9.03
	23	8	2.715	8.64
	1	9	3.169	10.09
	1	10	3.310	10.54
	1	11	3.272	10.41
	1	12	2.900	9.23
Mar. 27-28	1	13	2.758	8.78
Mar. 28	1	14	2.776	8.84
	1	15	2.685	8.55
	1	16	2.350	7.48
	2	17	2.051	6.53
	2	18	1.734	5.52
	2	19	1.619	5.15
Mar. 28-29	2	20	1.713	5.45
Mar. 29	2	21	1.239	3.94
	2	22	1.360	4.33
	3	23	1.171	3.73
Mar. 29-30	3	24	1.290	4.11
Mar. 30	3	25	1.122	3.57
	3	26	1.235	3.93
Mar. 30-31	4	27	1.254	3.99
Mar. 31	4	28	1.265	4.03
	4	29	1.282	4.08

<sup>1</sup>Snake weighed 6.09 kg. on Mar. 26, and 5.76 kg. on March 31, sometime after it was removed from respiration chamber. Weight assumed to have decreased to 5.82 kg. in periods 26 to 29.

<sup>2</sup>Based on curve in figure 54, page 224.

perature would be 3.54 calories and 1.062 grams of carbon dioxide, according to the general smoothed curve for all boas (fig. 54), and this baseline has been given in table 70. One hour after food, the carbon-dioxide production was 0.777 gram or actually lower than the assumed baseline, but thereafter it rapidly increased to a maximum of 3.310 grams 1 day and 3 hours after food. It then decreased and remained at a fairly con-

stant level between the twenty-third and the twenty-ninth periods, although this level was by no means as low as the assumed baseline. On the other hand, the metabolism 1 hour and 4 hours after food ingestion was actually lower than the level established on the fifth day in the

TABLE 71—*Metabolism of boa F during protein digestion*  
(24.1° C.; 539-gm. rabbit eaten May 2)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917 May 1	<i>days hrs.</i> 14	..	<i>gm.</i> 0.343	<i>cal.</i> 1.15
May 2	3	1	.530	1.69
	6	2	.875	2.79
	13	3	.954	3.04
May 2-3	19	4	1.031	3.28
May 3	1 5	5	.949	3.02
	1 12	6	1.186	3.78
May 3-4	1 19	7	1.188	3.78
May 4	2 0	8	1.428	4.55
	2 8	9	1.413	4.50
	2 14	10	1.467	4.67
Mar 4-5	2 20	11	1.612	5.13
May 5	3 2	12	1.473	4.69
	3 9	13	1.849	5.89
May 5-6	3 16	14	1.626	5.18
May 6	4 0	15	1.678	5.34
	4 6	16	1.198	3.81
	4 14	17	1.325	4.22
May 6-7	4 20	18	1.011	3.22
May 7	5 5	19	.932	2.97
	5 12	20	.973	3.10
May 7-8	5 20	21	.687	2.19
May 8	6 6	22	.800	2.55
	6 13	23	.741	2.36
May 8-9	6 20	24	.650	2.07
May 9	7 6	25	.751	2.39
	7 13	26	.774	2.46
May 9-10	7 21	27	.637	2.03
May 10	8 6	28	.848	2.70
	8 14	29	.707	2.25
May 10-11	8 21	30	.709	2.26
May 11	9 8	31	.966	3.07
May 11-12	9 16	32	.589	1.87
May 12	10 4	33	.562	1.79

<sup>1</sup>Snake weighed 5.73 kg. on May 1, 6.27 kg. on May 2, and 6.07 kg. on May 12 after it was removed from respiration chamber. Weight assumed to have decreased to 6.07 kg. in periods 32 and 33.

twenty-eighth and the twenty-ninth periods. It is probable that the body temperature of boa F was lowered when it was brought from the reptile house to the laboratory for the digestion experiment and sufficient time was not allowed for it to adjust itself to the temperature of 32° C. before beginning the experiment. The maximum heat production, 10.54 calories,

was 198 per cent above the baseline of 3.54 calories. From the constancy in the latter part of the curve for this experiment in figure 74 it would seem as if  $2\frac{1}{2}$  days after food the metabolism had reached a plateau at about 4 calories. One might assume that this level represented the baseline metabolism for this experiment, and for this reason the baseline has been indicated as 4 calories in figure 74, rather than the 3.54 calories given in table 70. But it is possible that this level of 4 calories represents the true after-effect of digestion, that the stimulus of the food was prolonged, and that if the experiment had been continued longer the metabolism would have decreased until finally, many days later, the hypothetical baseline (3.54 calories) assumed from the curve for all boas would have been reached.

The third digestion experiment was made with boa F on May 2 to 12 (table 71). A 539-gram rabbit, equivalent to 9 per cent of the boa's weight, was eaten on May 2. The snake had last fed 15 days before, that is, on April 17. The average environmental temperature during the digestive cycle was  $24.1^{\circ}$  C. The baseline metabolism at this temperature was determined in a 19-hour period on May 1, when the carbon-dioxide production was found to be 0.343 gram and the heat production 1.15 calories. The boa remained in the respiration chamber during the interval between the standard metabolism experiment on May 1 and the digestion experiment beginning on May 2. Three hours after the snake had eaten, the metabolism was higher than the baseline, the carbon-dioxide production being 0.530 gram as compared with a measured baseline of 0.343 gram. The maximum carbon-dioxide production, 1.849 grams, occurred in the thirteenth period or 3 days and 9 hours after food. Thereafter there was a fairly regular decrease in the metabolism, continuing until the end of the experiment.

The data for the digestion experiments of March 26 to 31 and May 2 to 12 are plotted in the two upper curves in figure 74 (p. 270). In both cases uniformity in metabolism appears to have been fairly well established toward the end of the experiment, although the metabolism does not reach the predigestive level indicated in tables 70 and 71. This suggests that perhaps the baselines were actually somewhat higher than those given in the tables. According to the curve for all boas in figure 54 (p. 224), the standard heat production at  $24^{\circ}$  C. would be 1.48 instead of 1.15 calories. The heat production after food ingestion in the May experiment at  $24^{\circ}$  C. reached a plateau of about 2 calories, or 35 per cent higher than 1.48 calories. This level of 2 calories has been indicated as the baseline in the uppermost curve in figure 74. If 2 calories does not represent the predigestive baseline, then unquestionably the stimulus due to the protein ingestion is a prolonged one, for this level of 2 calories appeared at about the sixth day and persisted for at least four days. If the snake's metabolism following food ingestion does not return to the computed predigestive level within 5 or 6 days, but reaches a higher level from which it no longer descends, how is this to be interpreted? One can conclude that the initial baseline is not *the true baseline*. It may be complicated by long fasting, although in the case of boa F in the experiment of May 2 to 12 the base-

line could not have been complicated by much prolonged fasting, for there had been a digestion experiment on March 26 to 31 and the snake had eaten again on April 17. Another explanation may be that the baseline of 1.15 calories is lower than it normally would have been at 24° C., because the snake, previous to the determination of this baseline, had been lying on a floor at a temperature several degrees lower than 24° C., and there may have been an after-effect of this low temperature. The sustained higher level of metabolism after food ingestion shown in this experiment of May 2 to 12 may be characteristic of the digestive cycle. Apparently there are two phases in the digestive cycle of the snake. In the first phase the metabolism responds quickly to the stimulus of the food, attaining a peak and then falling off. In the second phase the metabolism is sustained for a long period at a fairly constant level, higher than the predigestive level, and (although not yet proved by our data) then tends to fall back to the predigestive level. This metabolic level in the second phase is undoubtedly the result of the deposition of body tissue, probably in large part protein. When food is eaten by an animal in an amount equivalent to from 10 to 25 per cent of its own body weight, a large proportion of it is deposited as additional body tissue. If the animal subsequently fasts for a long period, this reserve will be drawn upon and the metabolism will ultimately return to the predigestive level, when the animal reaches a stage of reserves corresponding to that prevailing before the ingestion of the food. This emphasizes the concept stated earlier in this report (page 155) that one can not speak, without mental reservations, of the "basal metabolism" of a snake. Among the warm-blooded animals (except the surfeit-fed goose) such a great change, proportionately, in body tissue as that noted with the snake and in such a short time would hardly, if ever, occur.

#### Boa I

With boa I in April 1917 a protein digestive cycle at a low temperature averaging 18.3° C. was studied. The snake ate a 425-gram rabbit on April 24 equivalent to 7 per cent of its weight (less food), and the first period of observation began 13 hours later, the snake having been inside the respiration chamber during all this time. It probably had not eaten for 42 days, that is, since March 13. The standard metabolism of this boa at 19.7° C. had been determined on April 20-21 and found to be 0.73 calorie. From the curve for all boas (fig. 54, p. 224) the standard metabolism at 18.3° C., that of the digestion experiment, would be 0.70 calorie. We therefore feel justified in considering 0.70 calorie as the baseline for this April digestion experiment.

The results of the April digestion experiment, as well as the underlined values for the assumed baseline, are given in table 72. From this table it is seen that 13 hours after the snake ate, there was a pronounced rise in the carbon-dioxide production, from the baseline of 0.210 to 0.309 gram. The periods of observation in this experiment were continuous, but in the attempt to analyze more exactly the change in metabolism due to the ingestion of food, they were made too short. For this reason in the first

TABLE 72—*Metabolism of boa I during protein digestion*

(18.3° C.; 425-gm. rabbit eaten April 24)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	days hrs.		gm. 20.210	cal. 20.70
Apr. 25	13	1	.309	.98
	16	2	.588	1.87
	19	3	.591	1.88
	22	4	.471	1.50
Apr. 25-26	1 3	5	.191	.61
Apr. 26	1 10	6	.344	1.10
	1 13	7	.295	.94
	1 17	8	.258	.82
	1 22	9	.484	1.54
Apr. 26-27	2 3	10	.556	1.77
Apr. 27	2 8	11	.593	1.89
	2 14	12	.470	1.50
	2 18	13	.408	1.30
	2 22	14	.533	1.70
Apr. 27-28	3 3	15	.473	1.51
Apr. 28	3 8	16	.734	2.34
	3 12	17	.674	2.15
	3 16	18	.489	1.56
	3 21	19	.713	2.27
Apr. 28-29	4 3	20	.411	1.31
Apr. 29	4 9	21	.643	2.05
	4 17	22	.593	1.89
Apr. 29-30	5 1	23	.634	2.02
Apr. 30	5 11	24	.501	1.59
Apr. 30-May 1	5 22	25	.560	1.78
May 1	6 14	26	.593	1.89
May 1-2	7 2	27	.584	1.86
May 2	7 16	28	.638	2.03
May 2-3	7 22	29	.513	1.63
May 3	8 11	30	.585	1.86
May 3-4	8 21	31	.546	1.74
May 4	9 14	32	.524	1.67
May 4-5	10 2	33	.564	1.80
May 5-6	10 15	34	.456	1.45
May 6	11 7	35	.522	1.66
May 6-7	11 20	36	.371	1.18
May 7	12 11	37	.451	1.44
May 7-8	13 2	38	.556	1.77
May 8-9	13 16	39	.546	1.74
May 9	14 6	40	.551	1.75
May 9-10	14 19	41	.668	2.13
May 10	15 8	42	.587	1.87
May 10-11	16 3	43	.510	1.62
May 11-12	16 19	44	.441	1.40
May 12	17 10	45	.671	2.14

<sup>1</sup> Snake weighed 6.58 kg. on Apr. 25. Weight assumed to have decreased to 6.53 kg. in periods 41 to 45. Weighed 6.52 kg. on May 12, after removal from respiration chamber.

<sup>2</sup> Based on curve in figure 54, page 224.

18 periods and in the twentieth period the amount of carbon dioxide collected and weighed in the absorbers was in practically all instances less than 1 gram (the minimum amount considered desirable for accuracy) and in seven instances less than half a gram. The later periods were longer, however, and consequently in period 19 and in periods 21 to 45 more than 1 gram of carbon dioxide was collected in each instance. The shortness of the periods at the start of the experiment probably explains the extraordinarily low value of 0.191 gram of carbon dioxide recorded for the fifth period. In all probability there was not a real decrease in metabolism at this time, but the apparent decrease is due to some error

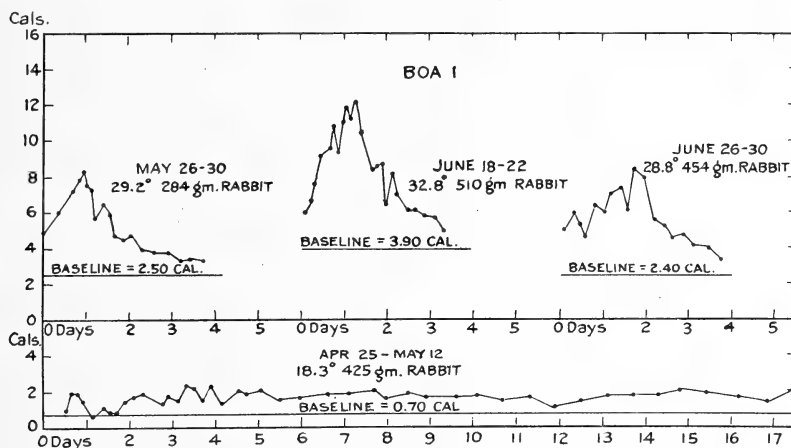


FIG. 75—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—Boa I.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake, are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

in weighing. It is to be regretted that duplicate weighings of the carbon dioxide could not have been made. It is perhaps surprising that such aberrant figures are not found more often.

The results of this digestion experiment of April 25 to May 12 are shown in the lowest curve in figure 75. It is difficult to locate the peak in this curve. There are several points that may be considered as highest, namely, during the fourth day, during the fifteenth day, and the last observation 17 days and 10 hours after food, or in other words, during periods 16, 17, 19, 41 and 45. On the assumption that the baseline is 0.70 calorie, we see that the metabolism is for the greater part of the time 100 and at times nearly 150 or 200 per cent above the baseline and there is no indication of a decrease in metabolism even after the seventeenth day. This again indicates the extraordinarily slow process of digestion of the snake at a low environmental temperature. The permanently increased metabolism resulting from deposited protein undoubtedly is a factor preventing the return of the metabolism to the predigestive baseline.



On May 12 boa I was returned to the reptile house. On May 26 to 30 a second protein digestion experiment was made at an average temperature of 29.2° C. Boa I ate a 284-gram rabbit on May 26, equivalent to 5 per cent of its weight, and the first observation began one hour later. The snake had not previously been fed since April 24, or for 32 days. The standard metabolism of boa I was determined prior to this digestion experiment on May 23 to 25, but the environmental temperature, 31.7° C.,

TABLE 73—*Metabolism of boa I during protein digestion*  
(29.2° C.; 284-gm. rabbit eaten May 26)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	<i>days hrs.</i>		<i>gm.</i>	<i>cal.</i>
.....	... ..	..	20.750	2.50
May 26-27	1	1	1.548	4.93
May 27	13	2	2.057	6.55
	18	3	2.289	7.29
	21	4	2.463	7.84
	23	5	2.606	8.29
	1 1	6	2.377	7.57
	1 3	7	2.300	7.32
May 27-28	1 5	8	1.782	5.67
May 28	1 10	9	2.015	6.41
	1 13	10	1.880	5.98
	1 16	11	1.472	4.69
	1 21	12	1.424	4.53
	2 1	13	1.477	4.70
May 28-29	2 8	14	1.253	3.99
May 29	2 14	15	1.189	3.78
	2 22	16	1.179	3.75
May 29-30	3 5	17	1.049	3.34
May 30	3 10	18	1.068	3.40
	3 17	19	1.048	3.34

<sup>1</sup> Snake weighed 6.29 kg. on May 26-27. Weight assumed to have decreased to 6.21 kg. in period 19. Weighed 6.18 kg. sometime after removal from respiration chamber on May 30.

<sup>2</sup> Based on curve in figure 54, page 224.

was 2.5 degrees higher than that obtaining during the digestion experiment. Consequently it seems most justifiable to use as a baseline for comparison the values obtained from the curve for all boas at 29.2° C. This corresponds to 0.750 gram of carbon dioxide and to 2.50 calories. As will be seen in table 73, the carbon-dioxide production was doubled in period 1 or in the first thirteen hours after eating. The increase continued until a maximum of 2.606 grams was reached 23 hours after food. The metabolism then began to fall off and reached a plateau by the fifteenth period or 2 days and 14 hours after food. Even 27 hours later it had not fallen materially below this plateau.

The results of this May experiment are also presented graphically in figure 75 (p. 277), expressed in calories. The heat production considered to represent the baseline was 2.50 calories. Since the plateau in heat production at the end of about three days was approximately 3.3 calories, the metabolism was still measurably above the assumed predigestive level. The curve indicates clearly the rapid decrease in metabolism following the peak effect. The maximum heat production was 8.29 calories,

TABLE 74—*Metabolism of boa I during protein digestion*  
(32.8° C.; 510-gm. rabbit eaten June 18)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	days hrs.		gm. <sup>2</sup> 1.170	cal. <sup>3</sup> 3.90
June 18	2	1	1.883	5.99
June 18-19	5	2	2.052	6.53
June 19	7	3	2.347	7.47
	11	4	2.847	9.06
	16	5	2.995	9.53
	18	6	3.381	10.76
	20	7	2.874	9.15
	23	8	3.411	10.86
	1 1	9	3.699	11.77
	1 3	10	3.513	11.18
June 19-20	1 6	11	3.789	12.06
June 20	1 9	12	3.213	10.23
	1 15	13	2.605	8.29
	1 18	14	2.675	8.51
	1 21	15	2.727	8.68
	1 23	16	1.985	6.32
	2 2	17	2.517	8.01
June 20-21	2 5	18	2.176	6.93
June 21	2 11	19	1.918	6.11
	2 15	20	1.889	6.01
	2 20	21	1.810	5.76
June 21-22	3 2	22	1.770	5.63
June 22	3 7	23	1.541	4.91

<sup>1</sup> Snake weighed 6.53 kg. on June 18. Weight assumed to have decreased to 6.32 kg. in periods 22 and 23. Weighed 6.29 kg. on June 22, sometime after removal from respiration chamber.

<sup>2</sup> Based on curve in figure 54, page 224.

that is, an increase of 232 per cent above the baseline. But the metabolism had not returned to the baseline at the end of the experiment. In this particular instance a relatively small rabbit weighing 284 grams was eaten, and yet the stimulus to the metabolism associated with digestion held on for some time.

A fasting experiment was obtained with boa I on June 4-5 at a very high temperature, 36° C. Still another digestion experiment (table 74 and fig. 75) was then carried out on June 18 to 22, at an average temperature

of 32.8° C., even higher than that of the May experiment. A 510-gram rabbit (8 per cent of the snake's weight) was eaten on June 18, two hours before the first observation. Boa I had not been fed since May 26 or for 23 days. The snake was in the respiration chamber during the night of June 17-18 at approximately the same temperature as that prevailing during the digestion experiment. The fasting experiment of May 23 to 25 at 31.7° C. gave a standard metabolism of 0.998 gram of carbon dioxide and 3.33 calories. The curve for all boas (fig. 54, p. 224)

TABLE 75—*Metabolism of boa I during protein digestion*  
(28.8° C.; 454-gm. rabbit eaten June 26)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1917	days hrs.		gm.	cal.
			<u>20.720</u>	<u>22.40</u>
June 26	2	1	1.573	5.01
June 26-27	7	2	1.830	5.82
June 27	10	3	1.668	5.31
	13	4	1.418	4.51
	19	5	1.962	6.25
	1 0	6	1.846	5.88
	1 4	7	2.197	6.99
June 27-28	1 9	8	2.277	7.25
June 28	1 13	9	1.890	6.02
	1 17	10	2.637	8.39
	1 22	11	2.499	7.95
	2 4	12	1.723	5.48
June 28-29	2 9	13	1.599	5.09
June 29	2 14	14	1.416	4.51
	2 20	15	1.446	4.60
June 29-30	3 2	16	1.277	4.06
June 30	3 10	17	1.231	3.92
	3 17	18	1.036	3.30

<sup>1</sup> Snake weighed 6.38 kg. on June 26. Weight assumed to have decreased to 6.31 kg. in periods 16 to 18. Weighed 6.29 kg. on June 30, some time after removal from respiration chamber.

<sup>2</sup> Based on curve in figure 54, page 224.

shows an average standard metabolism at 33° C. of 3.90 calories or 1.170 grams of carbon dioxide. Probably the metabolism indicated by this curve for all boas is more nearly representative of the true baseline for this digestion experiment, since the temperature of the digestion experiment, 32.8° C., is practically 33° C. The values derived from the curve in figure 54 have therefore been used for the baseline. From the results recorded in table 74 it can be seen that the metabolism 7 hours after eating was twice as great as the baseline. There was a continual, rapid rise until a peak was reached in the eleventh period, or 1 day and 6 hours after eating. At this time the maximum heat production was 12.06 calories or 209 per cent above the baseline. Thereafter there was a rapid

decrease, but the experiment was not continued long enough for the metabolism to reach even an approximate plateau, as there was a decrease in the last observation. In other words, at the end of 3½ days, although the temperature was high (32.8° C.), the baseline had not been reached, but in this particular case boa I had eaten a rabbit nearly twice as large as that in the preceding May experiment. The rectal temperature at the end of the experiment, on June 22, was 32.29° C., when the temperature of the respiration chamber was 32.39° and that of the room 23.0° C.

This experiment of June 18 to 22, in which the metabolism by no means returned to the baseline, was followed a few days later, June 26 to 30, by another digestion experiment at a somewhat lower temperature averaging 28.8° C. (table 75). A 454-gram rabbit (8 per cent of the boa's weight) was eaten on June 26, two hours before the first measurement began. Boa I was last fed 8 days before, or on June 18. The snake had been in the respiration chamber during the night of June 25-26 at probably a somewhat higher temperature than that obtaining during the digestion experiment. Since the baseline was not actually measured previous to this digestive cycle, the comparative values have been again derived from the curve for all boas, which shows at 28.8° C. an average standard heat production of 2.40 calories, corresponding to 0.720 gram of carbon dioxide. Two hours after the snake had eaten, the carbon-dioxide production had increased from 0.720 to 1.573 grams, that is, it was more than doubled. The increase continued steadily until the tenth period, 1 day and 17 hours after food, when the heat production (fig. 75) was at a maximum of 8.39 calories or 250 per cent higher than the baseline. Thereafter there was the characteristic rapid decrease, but a plateau in metabolism was not reached at the end of 3 days and 17 hours and the metabolism did not even approximate the calculated predigestive level. The rectal temperature of boa I at the end of the experiment on June 30 was 27.68°, the temperature of the respiration chamber was 27.58°, and that of the room 22.8° C.

#### BOA J

Four protein experiments were made with boa J, all at temperatures close to 29° C. The results are recorded in tables 76, 77 and 78. The first experiment (table 76) was from October 7 to 11, at which time the snake weighed 4.7 kg. When this snake was brought to the laboratory on October 6, it was reported that it had been fed September 25, but from the high metabolism during this particular digestive cycle there is every reason to believe that it had been fed since that time. The average temperature during the digestion experiment was 29.2° C. The standard metabolism was not measured immediately preceding the period of digestion, but two different series of measurements on October 24-25 and November 5-6, 1919, at temperatures closely approximating 29.2° C., gave results that confirm the average metabolism indicated by the curve for all boas at this temperature, that is, 2.50 calories or 0.750 gram of carbon dioxide. These values have therefore been used as the baseline for this first protein digestion experiment. The carbon-dioxide production during the first period of the digestion experiment was more than double the base-

TABLE 76—*Metabolism of boa J during protein digestion*  
(29.2° C.; fed probably Sept. 25<sup>1</sup>; 142-gm. guinea-pig  
eaten Oct. 11)

Date	Time since eating	Period	Per kg. <sup>2</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919	days hrs.		gm. 30.750	cal. 32.50
Oct. 7	16	1	1.896	6.03
	10	2	2.201	7.01
	16	3	3.308	10.53
	21	4	2.708	8.62
Oct. 7-8	1 3	5	2.199	7.00
Oct. 8	1 10	6	1.931	6.15
	1 16	7	2.155	6.86
	1 20	8	2.082	6.63
Oct. 9 <sup>4</sup>	2 8	1	1.733	5.52
	2 13	2	1.766	5.62
	2 18	3	1.683	5.36
	2 22	4	1.717	5.47
	3 2	5	2.003	6.38
Oct. 9-10	3 6	6	1.408	4.48
Oct. 10	3 12	7	1.807	5.75
	3 17	8	1.587	5.05
	3 21	9	2.052	6.53
Oct. 10-11	4 1	10	1.746	5.56
	4 6	11	1.555	4.95
Oct. 11	4 11	12	1.372	4.37
	4 16	13	1.529	4.87
Oct. 11 <sup>5</sup>	1	1	1.858	5.91
Oct. 11-12	4	2	1.827	5.82
Oct. 12	6	3	1.821	5.80
	11	4	1.878	5.98
	16	5	2.249	7.16
	19	6	2.229	7.10
	22	7	2.295	7.31
	1 1	8	2.726	8.68
Oct. 12-13	1 3	9	2.556	8.14
Oct. 13	1 6	10	2.007	6.39
	1 10	11	2.333	7.43
	1 15	12	2.933	9.34
	1 18	13	2.298	7.31
	1 20	14	2.238	7.12
	2 2	15	1.955	6.22
Oct. 13-14	2 6	16	1.738	5.53
	2 12	17	1.846	5.88
	2 16	18	1.674	5.33
	2 22	19	1.555	4.95
Oct. 14-15	3 4	20	1.530	4.87
Oct. 15	3 11	21	1.372	4.37
	3 16	22	1.321	4.20

<sup>1</sup> Boa reported as fed Sept. 25; results indicate later feeding. Assumed boa had been fed at 6 p.m., Oct. 6.

<sup>2</sup> Snake weighed 4.71 kg. on Oct. 6. Weight assumed to be 4.67 kg. on Oct. 9 and to have decreased to 4.63 kg. on Oct. 10-11, periods 10 to 13. Weighed 4.31 kg. on Oct. 11 after defecating and before eating. Weighed 4.45 kg. on Oct. 11, after eating. Weight assumed to have decreased to 4.40 kg. in periods 19 to 22. Weighed 4.39 kg. on Oct. 15, after removal from respiration chamber.

<sup>3</sup> Based on curve in figure 54, page 224.

<sup>4</sup> Boa remained in respiration chamber between Oct. 8 and Oct. 9.

<sup>5</sup> Ate 142-gm. guinea-pig between thirteenth period on Oct. 11 and first period of second series of observations beginning on Oct. 11.

line value of 0.750 gram. The peak occurred in the third period. Since the exact time after feeding and the amount of food are not known, the chief significance of this experiment is that it indicates a high metabolism at the start, followed by a decrease, and that the metabolism has not returned to the predigestive level at the end of the series of observations.

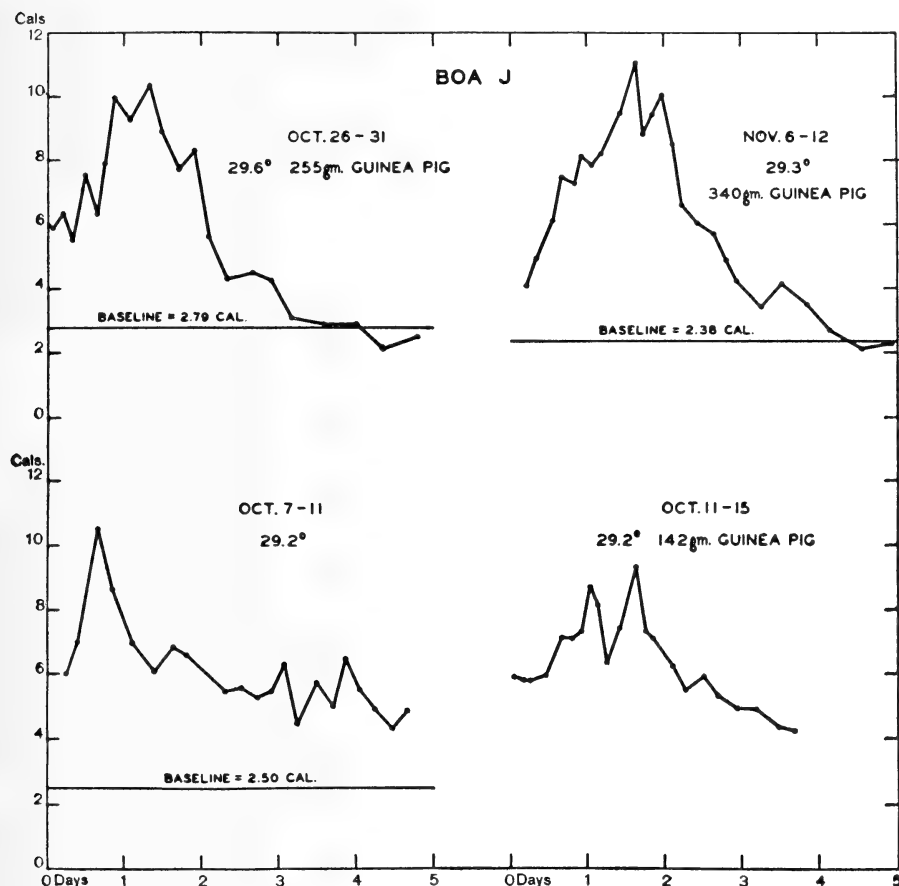


FIG. 76—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—Boa J.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

The periods were consecutive in all the protein experiments with boa J, but in this first series there was an interruption between the measurements on October 8 and those on October 9. The boa apparently remained in the respiration chamber during the interval, although, judging from the somewhat lowered temperature at the beginning of the first period on October 9, the chamber may have been opened. A large amount of feces was found when the chamber was opened on October 11. From the

graphic record of activity, it is thought that these feces were passed after the end of the experiment.

In figure 76 the results of this experiment of October 7 to 11 have been plotted, expressed in calories and compared with the baseline of 2.50 calories. The time after feeding is not exactly known (see page 281), but for purposes of discussion it has been assumed that the first measurement began 6 hours after feeding. The peak in the heat production was 10.53 calories or 321 per cent above the baseline. At the end of 4 days the metabolism had by no means returned to the assumed predigestive level and there was no indication of a plateau.

In spite of the fact that boa J's metabolism had not reached the assumed initial baseline on October 11, a 142-gram guinea-pig (3 per cent of its weight) was fed on October 11 and a second protein experiment was carried out from October 11 to 15, again at an environmental temperature of 29.2° C. (table 76 and fig. 76). Boa J had been taken out of the respiration chamber after the end of the thirteenth period on October 11, to remove excreta that had been voided following this period. It was weighed at 3<sup>h</sup>15<sup>m</sup> p.m. on this same day and returned to the chamber. The guinea-pig was then given to it, but the snake did not swallow it until about 7<sup>h</sup>20<sup>m</sup> p.m. Strictly speaking, there is no baseline for comparison with the results of this second October experiment, other than the last measurement obtained in the preceding series, when the carbon-dioxide production was 1.529 grams. Within one hour after the guinea-pig was eaten the snake's carbon-dioxide production had increased. It reached a peak of 2.933 grams in the twelfth period or 1 day and 15 hours after food. The metabolism then decreased and the last two values are below that for period 13 of the first digestion experiment, although the metabolism can hardly be said to have reached a definite plateau. The last result, 1.321 grams, is measurably above the baseline of 0.750 gram derived from the curve for all boas.

The curve for this experiment of October 11 to 15 (fig. 76) shows that the usual immediate sharp rise in metabolism at the high environmental temperature is here delayed, and that the metabolism at the start remains at a level of about 5.9 calories for several hours. The rise in metabolism then begins, but there is an aberrant result in the tenth period, for which no adequate explanation is at hand. The peak in heat production, 9.34 calories, although indicated in figure 76 as having occurred somewhat after 1½ days, that is, in the twelfth period, may possibly have taken place somewhat earlier. Owing to the uncertainty of the baseline, the percentage increase in metabolism can not be calculated. The peak of 9.34 calories is, however, lower than the peak of 10.53 calories noted in the preceding experiment, when an unknown amount of food was eaten. The curve shows clearly that the metabolism had not reached a constant level at the end of 3½ days. On October 15 it was found that boa J was getting ready to shed. The skin was shed on October 23.

On October 26 another protein digestion experiment was begun with boa J at practically the same temperature, averaging 29.6° C. (table 77 and fig. 76). This was fortunately preceded by standard metabolism

observations on October 24-25 at the same temperature, when the carbon-dioxide production was found to be 0.835 gram and the heat production 2.79 calories. The last observation in the preceding digestion experiment, namely, on October 15, showed a heat production of 4.20 calories 3 days and 16 hours after food. Boa J was kept at approximately the same temperature for the 10 days following October 15, and at the end

TABLE 77—*Metabolism of boa J during protein digestion*  
(29.6° C.; 255-gm. guinea-pig eaten Oct. 26)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919 Oct. 24-25	days hrs. 13	.....	gm. 0.835	cal. 2.79
Oct. 26	2	1	1.855	5.90
Oct. 26-27	5	2	2.006	6.39
Oct. 27	8	3	1.715	5.46
	12	4	2.371	7.55
	16	5	2.002	6.37
	18	6	2.484	7.91
	21	7	3.100	9.87
Oct. 27-28	1 2	8	2.899	9.23
Oct. 28	1 8	9	3.248	10.34
	1 12	10	2.779	8.85
	1 17	11	2.440	7.77
	1 22	12	2.616	8.33
Oct. 28-29	2 2	13	1.770	5.63
Oct. 29	2 8	14	1.348	4.29
	2 16	15	1.413	4.50
	2 22	16	1.327	4.22
Oct. 29-30	3 4	17	.980	3.12
Oct. 30	3 14	18	.913	2.91
Oct. 30-31	4 0	19	.909	2.89
Oct. 31	4 8	20	.667	2.12
	4 19	21	.798	2.54

<sup>1</sup> Snake weighed 3.92 kg. on Oct. 24-25, 4.18 kg. on Oct. 26, and 4.18 kg. on Oct. 31, after it was removed from respiration chamber.

of this time its standard heat production was 2.79 calories. Consequently it may be assumed that had the experiment of October 11 to 15 been continued without interruption until October 24-25, the fall from 4.20 to 2.79 calories would have been definitely established.

Boa J was not taken out of the respiration chamber between the standard metabolism observations on October 24-25 and the observations during the following digestive cycle. A guinea-pig weighing 255 grams or 7 per cent of the actual body weight of the snake (a fairly large meal) was eaten on October 26. The boa had not been fed since October 11. There was a characteristic rise in metabolism which began within 2 hours after food, and the baseline value of 0.835 gram of carbon dioxide was immedi-



ately more than doubled to 1.855 grams. The peak, 3.248 grams, occurred in the ninth period, or 1 day and 8 hours after food was taken. There then followed the characteristic, rather rapid fall in carbon-dioxide production. In the last two periods low values were found, averaging 0.733 gram, that is, somewhat below the measured baseline of 0.835 gram. This is the first instance in the digestion experiments thus far reported in which the snake's metabolism actually returned to the measured predigestive

TABLE 78—*Metabolism of boa J during protein digestion*

(29.3° C.; 340-gm. guinea-pig eaten Nov. 6)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919 Nov. 5-6	<i>days hrs.</i> 10	.....	<i>gm.</i> 0.713	<i>cal.</i> 2.38
Nov. 6-7	5	1	1.279	4.07
Nov. 7	8	2	1.567	4.99
	13	3	1.929	6.14
	16	4	2.359	7.51
	20	5	2.283	7.27
	22	6	2.559	8.15
	1 1	7	2.463	7.84
Nov. 7-8	1 4	8	2.577	8.20
Nov. 8	1 10	9	2.994	9.53
	1 15	10	3.475	11.06
	1 17	11	2.768	8.81
	1 20	12	2.963	9.43
	1 23	13	3.153	10.04
	2 2	14	2.667	8.49
Nov. 8-9	2 5	15	2.074	6.60
Nov. 9	2 10	16	1.898	6.04
	2 15	17	1.807	5.75
	2 19	18	1.528	4.86
Nov. 9-10	2 22	19	1.319	4.20
Nov. 10	3 6	20	1.074	3.42
	3 12	21	1.306	4.16
	3 20	22	1.096	3.49
Nov. 10-11	4 3	23	.862	2.74
Nov. 11	4 13	24	.684	2.18
Nov. 11-12	4 22	25	.724	2.30

<sup>1</sup> Snake weighed 3.98 kg. on Nov. 5-6, 4.32 kg. on Nov. 6-7, and 4.32 kg. on Nov. 12, after it was removed from respiration chamber.

level. This experiment, together with evidence secured with other snakes, indicates that the period of digestion with snakes is much longer than we at first thought. It is possible that the after-effect of the food on October 11 may have held over until October 24, especially since the food on October 11 was preceded by a meal not long before. But in any event the metabolism of boa J has now for the first time returned to the initial starting point. The curve for the digestive cycle of October 26 to 31 in figure 76 (p. 283) shows the characteristic picture of a rapid rise in heat

production, a peak of 10.34 calories at the end of 1 day and 8 hours, or an increase of 270 per cent above the baseline, and then a rapid fall to a level approximately the same as the measured predigestive level.

After the third October experiment, boa J was maintained at the same environmental temperature, *i.e.*, about 30° C., and a fourth protein experiment was carried out on November 6 to 12 (table 78). A guinea-pig weighing 340 grams, or 9 per cent of the snake's weight, was eaten on November 6. The snake had last been fed on October 26. The measured baseline obtained on November 5-6 at 29.0°, or nearly the same temperature as the digestion experiment, was 0.713 gram of carbon dioxide and 2.38 calories. This baseline determined on November 5-6 is lower than that obtained on October 24-25, which in turn is lower than that of August 22-24. But the November baseline closely approaches the metabolism indicated by the curve for all boas at 29° C., namely, 0.735 gram of carbon dioxide and 2.45 calories. The standard metabolism as measured on November 5-6 has therefore been considered as the baseline for comparison. Within 5 hours after the snake had eaten the guinea-pig, the carbon-dioxide production was nearly doubled and continued increasing until the maximum was reached in the tenth period, or 1 day and 15 hours after food. Thereafter the characteristic fall in metabolism occurred, and in the last two periods near the end of the fifth day the carbon-dioxide production was practically the same as the initial, measured baseline. This is, therefore, the second instance with boa J in which the metabolism following protein ingestion returned to the measured, initial, predigestive level and, singularly enough, in both instances the baseline was reached within 5 days. These two experiments indicate that had the protein experiments been continued long enough with the other snakes, the metabolism could reasonably have been expected to return to the predigestive level. Why there was this rapid return with boa J can not be explained. One would think that, particularly in the experiment of November 6 to 12 after a large meal, there would have been every reason for a prolonged after-effect of digestion. But it is clear that such a prolonged after-effect did not exist. The maximum heat production, as shown by the upper right-hand curve in figure 76 (p. 283) was 11.06 calories, that is, an increase of 365 per cent above the baseline of 2.38 calories. This is the largest increase that has been found thus far in these protein experiments (except in the experiment of March 10 to 15 with the small Indian python, which included the effect of prolonged fasting), but is quite to be expected when one considers the large animal eaten in proportion to the body weight.

#### Boa K

Boa K was a small snake weighing only about 4 kg. It was used for one protein experiment at a high temperature, averaging 29.4° C. A guinea-pig weighing 510 grams was fed to the snake at 2<sup>h</sup>15<sup>m</sup> p.m., August 4, and a second guinea-pig weighing 567 grams at 3<sup>h</sup>30<sup>m</sup> p.m., the same day. The first observation began one hour after the food had been consumed, and the measurements continued without interruption through August 9. Apparently the boa was quiet throughout this time, but both

guinea-pigs were disgorged, possibly during period 31 on August 9, although the position of the snake in the respiration chamber was such that the activity recording device did not indicate when the food was disgorged. The respiration chamber was opened at noon on August 9

TABLE 79—*Metabolism of boa K during protein digestion*

(29.4° C.; 510-gm. and 567-gm. guinea-pig eaten Aug. 4)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919	days hrs.		gm.	cal.
July 28-Aug. 2	12	.....	<sup>2</sup> 1.20	<sup>2</sup> 4.00
Aug. 4	1	1	1.521	4.84
Aug. 4-5	5	2	1.744	5.55
Aug. 5	9	3	1.820	5.79
	13	4	1.616	5.14
	17	5	2.305	7.34
	22	6	2.826	9.00
	1 2	7	3.415	10.87
Aug. 5-6	1 6	8	4.483	14.27
Aug. 6	1 9	9	4.737	15.08
	1 12	10	5.430	17.28
	1 15	11	5.182	16.49
	1 18	12	5.463	17.39
	1 21	13	5.248	16.70
	2 0	14	5.578	17.75
	2 3	15	5.370	17.09
	2 5	16	5.098	16.23
Aug. 6-7	2 7	17	4.988	15.88
Aug. 7	2 13	18	5.145	16.38
	2 16	19	4.900	15.60
	2 19	20	4.839	15.40
	2 22	21	4.836	15.39
	3 1	22	4.277	13.61
	3 4	23	4.634	14.75
Aug. 7-8	3 7	24	4.083	13.00
Aug. 8	3 13	25	3.696	11.76
	3 16	26	2.574	8.19
	3 21	27	2.968	9.45
	4 1	28	3.181	10.13
Aug. 8-9	4 5	29	2.707	8.62
Aug. 9	4 9	30	3.156	10.05
	4 14	31	2.873	9.14

<sup>1</sup>Snake weighed 3.8 kg. on July 28 and Aug. 2, and 4.22 kg. on Aug. 4. The latter weight includes weight of 510-gm. guinea-pig only. Weight assumed to have decreased to 3.98 kg. in periods 27 to 31. Weighed 3.91 kg. on Aug. 9, sometime after removal from respiration chamber.

<sup>2</sup>Corrected to 29.4° C. See page 251.

because of the foul odor coming from the first sulphuric-acid vessel, when it was being changed. It was found that one guinea-pig had been almost entirely absorbed and the other about half. The body weight recorded at the beginning of the experiment on August 4 therefore includes the weight of only one guinea-pig (510 grams). The standard metabolism of

boa K had been measured on August 1-2. The snake had then been taken to the reptile house and was brought back and put into the respiration chamber at noon on August 4. On August 9 at the end of the experiment, it was found that the boa's eyes were clouded and it was almost ready to shed its skin. It was reported also on August 18 that the snake was

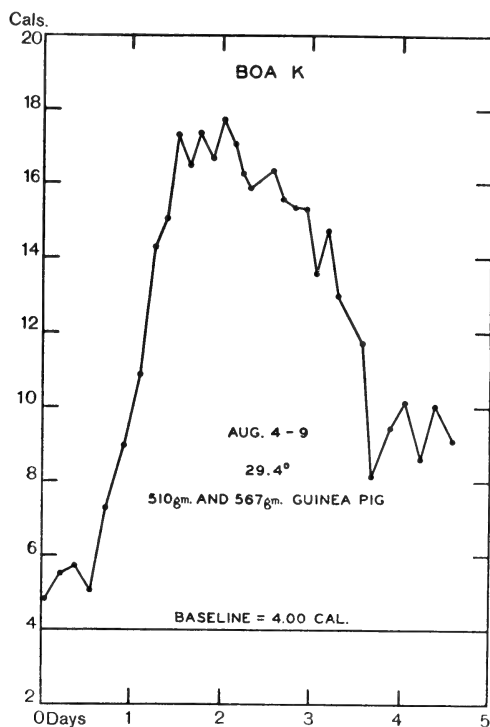


FIG. 77—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—BOA K.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake, are indicated on chart near curve. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

about to shed. Late in September boa K was unable to retain food and appeared very thin.

Standard values for comparison with the protein experiment with boa K were secured between July 28 and August 2, averaging 1.067 grams of carbon dioxide and 3.56 calories. The average temperature, however, was 28.5° C., or a degree lower than that of the digestion experiment. Hence it is necessary to correct for the difference in temperature. The baseline can not be derived from the curve for all boas, since this curve shows a heat production at 28.5° C. of 2.30 instead of 3.56 calories. There is

evidently something specifically individual in the metabolism of boa K that makes it unjustifiable to use the baseline derived from the curve for all boas, especially since three fairly well-agreeing standard values were actually obtained. According to the curve for all boas, the heat production increases 22 per cent for each degree increase in environmental temperature between 20° and 30° C. The corrected baseline values are therefore 1.2 grams of carbon dioxide and 4 calories.

The two guinea-pigs had a total weight of 1077 grams, equivalent to 29 per cent of the snake's own body weight, a very large meal. Within one hour after eating, as will be seen from table 79, the carbon-dioxide production was increased, but not doubled until the seventeenth hour. The peak was reached in the fourteenth period or in 2 days. There was then a rapid fall, with a tendency for uniformity in the last four or five periods, but since in these periods the carbon-dioxide production averaged 2.977 grams as compared with the assumed baseline of 1.2 grams, there is with boa K, as there was with the other snakes except boa J, clear evidence of a sustained after-effect of digestion, since the metabolism even after 4½ days was at a much higher level than the supposed predigestive level.

The results of the protein experiment with boa K, expressed in calories, have been plotted in figure 77, compared with the assumed baseline of 4 calories. One sees that after about 12 hours there was a rapid rise in the heat production to a peak of between 17 and 18 calories, which was sustained for about 12 hours. There was then the usual rapid fall, with later a tendency for a plateau to be reached, but considerably higher than the baseline. The maximum heat production, 17.75 calories, was 344 per cent above the baseline of 4 calories, next to the highest increase thus far noted. This is undoubtedly to be accounted for, in part at least, by the unusually large meal.

#### GOPHER SNAKES

Although of small size, gopher snakes have proved to be of considerable economic importance because of their activity in destroying rodents, and in the zoological park they are considered good feeders. Hence protein digestion experiments were made with two gopher snakes. The first, gopher snake A, weighed about 3 kg. and was studied on September 5 to 7 at an average temperature of 29.1° C. The standard metabolism of this snake was not determined preceding the digestive cycle. On February 5 to 7 the standard metabolism of three gopher snakes was measured, but at a temperature one degree higher than that of this digestion experiment. In lieu of better measurements, the baseline has been taken from the curve for all gopher snakes shown in figure 63 (p. 237), namely, 1.470 grams of carbon dioxide and 4.90 calories. On the afternoon of September 3 the snake ate 3 sparrows. It is not known how long gopher snake A had fasted before September 3. In general, however, these snakes feed fairly frequently in captivity, about every four or five days. The snake was put into the respiration chamber at 4 p.m., September 4, but the metabolism was not measured until the next day, that is, 1 day and 7 hours after eating. At this time, as will be seen from table 80, the carbon-

dioxide production was more than twice the baseline value and, indeed, was at the highest point observed during this experiment. It then decreased, but extremely irregularly, to 1.422 grams or close to the baseline value of 1.470 grams.

This first protein experiment was considered an orientation experiment, and a second experiment was carried out with gopher snake A from September 11 to 18 at an average temperature of 29.3° C. (table 81). In the first experiment the weight of the sparrows was unknown. In the second experiment the snake ate a 142-gram guinea-pig, which represented 5 per cent of its body weight. It had not eaten since September 3. The

TABLE 80—*Metabolism of gopher snake A during protein digestion*  
(29.1° C.; ate 3 sparrows Sept. 3)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919	days hrs.		gm.	cal.
	.....	.....	<sup>2</sup> 1.470	<sup>4</sup> 4.90
Sept. 5	1 7	1	3.037	9.67
	1 16	2	2.917	9.28
	1 21	3	1.583	5.04
Sept. 5-6	2 1	4	1.401	4.46
Sept. 6	2 7	5	1.354	4.31
	2 14	6	<sup>3</sup> 2.418	<sup>5</sup> 7.70
	2 20	7	1.474	4.69
Sept. 6-7	3 4	8	1.722	5.48
Sept. 7	3 13	9	1.422	4.53

<sup>1</sup> Snake weighed 2.89 kg. on Sept. 4. Weight assumed to be 2.87 kg. in periods 7 to 9. Not weighed at end.  
<sup>2</sup> Based on curve in figure 63, page 237.  
<sup>3</sup> Active.

experiment began one hour after the guinea-pig had been consumed. The metabolism presumably of gopher snake A was measured on September 8-9 at 28.5° C., when the snake had been 5 days without food. The carbon-dioxide production averaged 1.228 grams and the heat production 4.09 calories. These values corrected to 29.3° C., according to the curve for gopher snakes in figure 63 (p. 237), would be 1.440 grams and 4.80 calories, respectively. These corrected values have been accepted for the baseline. The carbon-dioxide production, although not above the baseline one hour after the guinea-pig was eaten, increased rapidly to a maximum of 4.050 grams in the fourteenth hour. It then fell off, and by the sixth day tended to reach a plateau of not far from 1.7 grams with, however, an occasional increase not ascribable, so far as was known, to any activity. The carbon-dioxide production remained measurably above the accepted baseline of 1.440 grams through the twenty-seventh period or into the seventh day.

The results of the digestion experiment of September 11 to 18 have been plotted in figure 78. Here one sees the characteristic rise in heat production to a peak of 12.89 calories, an increase of 169 per cent above the assumed baseline of 4.80 calories. It would appear that with this snake, as with so many of the others, there was a tendency for the metabolism

TABLE 81—*Metabolism of gopher snake A during protein digestion*

(29.3° C.; 142-gm. guinea-pig eaten Sept. 11)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919 Sept. 8-9 <sup>2</sup>	days hrs. 5	.....	gm. 21.440	cal. 24.80
Sept. 11	1	1	1.302	4.14
	4	2	2.472	7.87
Sept. 11-12	7	3	2.970	9.45
Sept. 12	11	4	3.131	9.97
	14	5	4.050	12.89
	18	6	3.802	12.10
	21	7	3.294	10.48
	1 2	8	2.916	9.28
Sept. 12-13	1 7	9	2.624	8.35
Sept. 13	1 13	10	2.560	8.15
	1 19	11	1.907	6.07
	2 1	12	1.621	5.16
Sept. 13-14	2 8	13	1.602	5.10
Sept. 14	2 17	14	1.962	6.25
	3 0	15	1.701	5.41
Sept. 14-15	3 6	16	1.886	6.00
Sept. 15	3 15	17	2.215	7.05
	3 23	18	2.028	6.46
Sept. 15-16	4 6	19	1.872	5.96
Sept. 16	4 13	20	2.014	6.41
	4 22	21	1.857	5.91
Sept. 16-17	5 4	22	1.600	5.09
Sept. 17	5 10	23	1.690	5.38
	5 19	24	1.786	5.68
	6 1	25	1.810	5.76
Sept. 17-18	6 9	26	1.490	4.74
Sept. 18	6 18	27	1.714	5.46

<sup>1</sup>Snake weighed 2.86 kg. on Sept. 8-9 and 3.01 kg. on Sept. 11. Weight assumed to have decreased to 2.95 kg. in periods 25 to 27. Weighed 2.95 kg. on Sept. 18, after removal from respiration chamber.

<sup>2</sup>Corrected to 29.3° C.

to reach a plateau quickly after the peak effect of digestion, but measurably higher than the baseline. There was then a second considerable rise in heat production, which continued until the end of the sixth day. Gopher snake A was about to shed its skin when returned to the reptile house on September 18.

The next experiment was made with gopher snake B, weighing nearly one kilogram less than gopher snake A (table 82). This snake, on Sep-

tember 23, ate two guinea-pigs weighing 142 grams, or 7 per cent of its own body weight. It is not known how long before September 23 it had last been fed. It was brought from the reptile house to the laboratory just after being fed and had recently shed its skin. No standard metabolism measurements are available for this snake. Judging from the curve for all gopher snakes in figure 63 (p. 237), the standard metabolism at

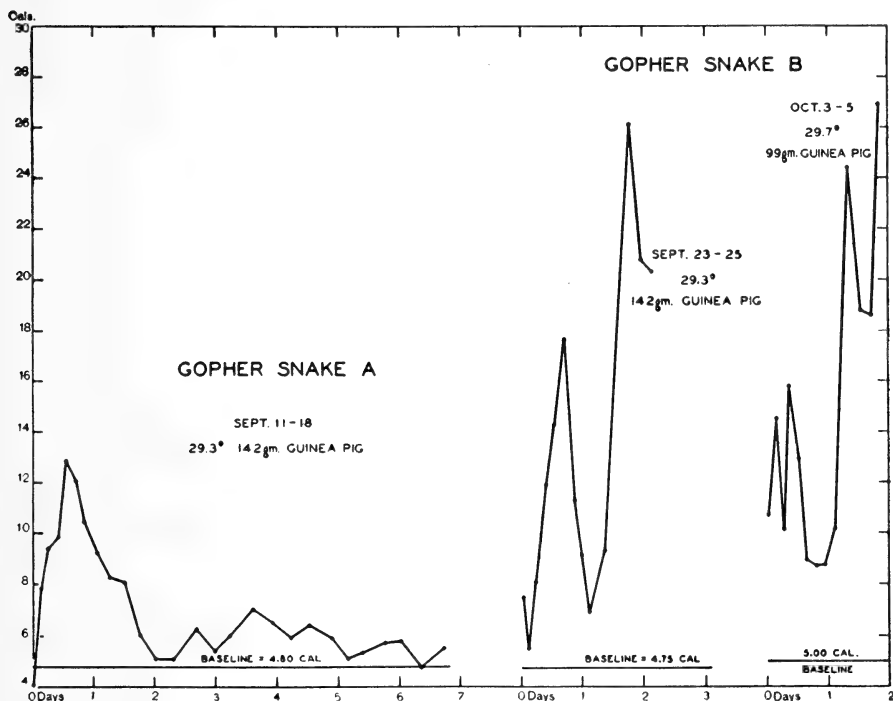


FIG. 78—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—GOPHER SNAKES A AND B.

Date of digestion experiment, average environmental temperature during experiment, and kind and amount of protein eaten by snake are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

29.3° C., the average temperature of this digestion experiment, would be 4.75 calories, corresponding to 1.425 grams of carbon dioxide. There was a marked increase in carbon-dioxide production one hour after eating, which may have been due to the activity incidental to constriction and swallowing. There is, however, a tendency for a steady rise thereafter to a peak of 5.537 grams at the seventeenth hour. The metabolism then began to return toward the assumed predigestive level, but underwent a tremendous increase in the eleventh period as a result of activity. The snake began to be active near the end of period 10 and was very active much of the time in the succeeding periods. When the respiration chamber was finally opened on September 25, a large mass of feces and partly



TABLE 82—*Metabolism of gopher snake B during protein digestion*  
(29.3° C.; 2 guinea-pigs weighing 142 gm. eaten Sept. 23)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919	days hrs.		gm.	cal.
	.. ..	...	<sup>2</sup> 1.425	<sup>2</sup> 4.75
Sept. 23	1	1	2.344	7.46
	3	2	1.725	5.49
Sept. 23-24	6	3	2.546	8.10
Sept. 24	10	4	3.748	11.93
	13	5	4.474	14.24
	17	6	5.537	17.62
	21	7	3.571	11.36
	1 0	8	2.882	9.17
	1 3	9	2.180	6.94
Sept. 24-25	1 9	<sup>3</sup> 10	2.935	9.34
Sept 25	1 18	11	8.178	26.03
	1 23	12	6.505	20.71
	2 3	13	6.353	20.22

<sup>1</sup>Snake weighed 2.18 kg. on Sept. 23. Weight assumed to have decreased to 2.04 kg. in periods 11 to 13. Weighed 2.04 kg. on Sept 25, after removal from respiration chamber.

<sup>2</sup>Based on curve in figure 63, page 237.

<sup>3</sup>Active near end of period 10 and very active much of the time in succeeding periods.

TABLE 83—*Metabolism of gopher snake B during protein digestion*  
(29.7° C.; 99-gm. guinea-pig eaten Oct. 3)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919	days hrs.		gm.	cal.
	.. ..	...	<sup>2</sup> 1.50	<sup>2</sup> 5.00
Oct. 3-4	1	1	3.357	10.69
Oct. 4	4	2	4.550	14.48
	7	3	3.185	10.14
	9	4	4.958	15.78
	13	5	4.058	12.92
	16	6	2.795	8.90
	20	7	2.730	8.69
Oct. 4-5	23	8	2.749	8.75
Oct. 5	1 3	9	3.198	10.18
	1 8	<sup>3</sup> 10	7.637	24.31
	1 13	11	5.878	18.71
	1 17	12	5.812	18.50
	1 20	13	8.413	26.78

<sup>1</sup>Snake weighed 2.11 kg. on Oct. 3. Weight assumed to have decreased to 1.96 kg. in periods 11 to 13. Weighed 1.96 kg. on Oct. 5, after removal from respiration chamber.

<sup>2</sup>Based on curve in figure 63, page 237.

<sup>3</sup>Active nearly all of period 10 and at beginning of period 11.

digested food that had been disgorged were found in the chamber. This undoubtedly accounts for the activity.

The curve for this experiment of September 23 to 25 is shown in figure 78. Only the first part of this curve can be considered as truly representative of the effect of digestion, and the high peak of 26 calories is to be disregarded except as an illustration of the height to which the metabolism can be increased by activity and other processes. Considering that the real peak is 17.62 calories, we see that the increase above the baseline of 4.75 calories is 271 per cent. The experiment is, however, complicated by the upset in digestion.

Shortly after, another experiment was carried out with gopher snake B on October 3 to 5, at an average temperature of 29.7° C. The snake ate a 99-gram guinea-pig equivalent to 5 per cent of its own body weight at 10 p.m. on October 3. It probably had not been fed since September 23, or for 10 days. It had been put into the respiration chamber at noon on October 3 and the first experimental period began at 10<sup>h</sup>55<sup>m</sup> p.m. or one hour after the guinea-pig was eaten. The results are recorded in table 83. The baseline at 29.7° C., as derived from the curve for gopher snakes (fig. 63, p. 237), has been assumed to be 5.0 calories or 1.50 grams of carbon dioxide. The carbon-dioxide production increased immediately after food to 3.357 grams or nearly two and one-half times that of the assumed baseline. It is questionable whether this snake was in a normal condition. The effect of the previous ingestion of food on September 23 may not have entirely disappeared at the time this October experiment began. The irregularity of the curve for this experiment (fig. 78) is striking, and the effect of activity in the tenth and the following periods is marked. The active periods in these digestion experiments have not been eliminated but are recorded in the tables, and the activity has been commented upon to explain the high values. Inasmuch as the digestion experiment of October 3 to 5 was complicated by activity in some periods, it is undesirable to compute the maximum percentage increase in metabolism as a result of the protein ingestion. The peak effect of digestion was substantially of the same order in the October experiment with gopher snake B as in the experiment of September 23 to 25, although on October 3 the snake ate one guinea-pig weighing only 99 grams, as compared with the two guinea-pigs weighing 142 grams eaten on September 23.

The general picture of the protein digestion experiments with these two gopher snakes is that there is a rapid rise in metabolism due to the ingestion of food. Only in the experiment of September 11 to 18 with gopher snake A does the metabolism return approximately to the baseline following digestion.

#### 1931 PYTHON

On January 24, at the conclusion of the experiment in the respiration chamber, the 1931 python was given two guinea-pigs weighing, respectively, 624 and 567 grams, and the metabolism was measured on six days thereafter at an environmental temperature held practically constant at 31° C. The two guinea-pigs, weighing together 1.2 kg., represent a meal equivalent to 22 per cent of the body weight of the animal—a very large

amount of food. The body weight underwent practically no change in the ten days during which the experiment continued, doubtless due to the fact that the python was occasionally given access to water when removed from the respiration chamber between the respiration experiments. The results of these observations during the digestion period are shown in detail in table 55 (p. 208), are summarized as average values in table 84, and are plotted on the basis of the heat production per unit of body weight in figure 79. The metabolism three days after food, on January 27, was extremely high, averaging 21.18 calories per kilogram of body weight per 24 hours. As time progressed, the heat production decreased until on the tenth day after food it averaged as low as 3.71 calories. According to the curve in figure 47 (p. 212) indicating the general trend of the standard

TABLE 84—*Metabolism of 1931 python during protein digestion*<sup>1</sup>

Date	Time since eating	Body weight	Periods		R. Q.	Temperature of—		Heat produced per kg. per 24 hours
			Total number	Average length <sup>2</sup>		Respiration chamber	Rectum	
1931	<i>days hrs.</i>	<i>kg.</i>		<i>mins.</i>		°C.	°C.	<i>cal.</i>
Jan. 27	2 18	6.5	4	3	0.72	31.9	35.6	21.18
Jan. 29	4 18	6.5	4	6	.58	31.3	....	17.60
Jan. 30	5 19	6.6	4	7	.74	31.1	....	7.67
Jan. 31	6 17	6.5	4	8	.73	32.9	34.0	9.05
Feb. 2	8 16	6.6	4	8	.74	30.9	32.5	5.74
Feb. 3	9 18	6.4	3	10	.75	31.4	....	3.71

<sup>1</sup>Two guinea-pigs weighing 624 and 567 grams, respectively, were eaten on Jan. 24.

<sup>2</sup>The length of these periods is at first sight challenging. Reference to description of technique employed (see page 36) shows that the method of collecting the sample of chamber air necessitated short periods. The certainty of the measurement is guaranteed by the fact that there were from 3 to 4 well-agreeing periods on each date, the average oxygen value for which we have used as the basis for each day's computation.

metabolism of the 1931 python at different environmental temperatures, the standard heat production at 31° would be about 3 calories per kilogram of body weight per 24 hours. The python's metabolism had therefore nearly returned to the baseline on the tenth day. The most striking feature of this experiment is the enormous increase in heat production as a result of the digestive activity, *i.e.*, 606 per cent of the assumed baseline. What happened on the first and second days after the food ingestion is not known. Undoubtedly the digestive processes are moderately slow at the start, even at a high temperature, but certainly for a short period of time on the third day after food the measured metabolism at 31° was over 21 calories, or seven times the standard metabolism at this temperature. On the sixth and seventh days the metabolism was nearly three times the standard value and, indeed, throughout the entire period of observation, that is, from the third to the tenth day after food or for one week the heat production was extremely high.

It was impracticable with the time at our disposal to measure the total increment in heat production after the ingestion of food until the return to

the baseline and thus compute the approximate specific dynamic action of the protein. The important point is, however, that undoubtedly during the process of digestion there is a great increase in the snake's heat production. This increase is reflected in the rectal temperatures, which were somewhat higher than the environmental temperature on the days during the peak of digestion. It is likewise reflected in the relatively high skin temperatures (p. 85). Unquestionably, therefore, sensible heat is given

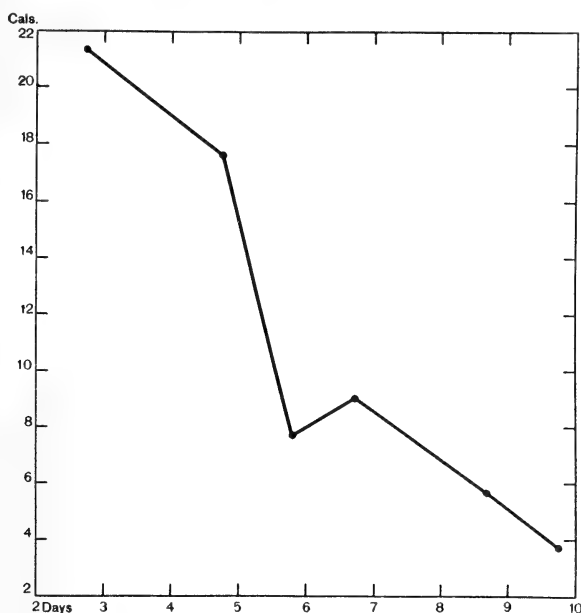


FIG. 79—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER PROTEIN INGESTION—1931 PYTHON.

Python ate two guinea-pigs weighing 624 and 567 grams, respectively. First metabolism measurement was made 2 days and 18 hours after food was eaten. Average environmental temperature during digestion experiment was 31.6° C. *Standard* heat production of this snake at 31° C. was about 3 calories per kilogram of body weight per 24 hours.

off during the period of digestion. This increased heat production was not contaminated by the effect of muscular motion as such in this particular instance, for the 1931 python was not observed to be any more active during the period of digestion than at any other time.

#### SUMMARY OF PROTEIN DIGESTION EXPERIMENTS WITH SNAKES

The presentation of the results of these protein experiments in the foregoing pages has necessarily been divided between the different snakes actually employed in the tests. To summarize these results for quick reference, an abstract of the data is given in table 85 indicating the kind

and amount of food eaten in each experiment, what percentage the food was of the snake's own body weight, the time after food ingestion when the metabolism reached its peak, the maximum percentage increase in heat production above the predigestive baseline, and the average environmental temperature prevailing during the experiment. Although the food eaten was usually a rabbit—occasionally a pigeon, guinea-pig, or sparrow—for

TABLE 85—Summary of protein digestion experiments

Snake	Date of experiment	Food <sup>1</sup>		Time at which metabolism reached peak	Maximum increase in heat production above baseline	Environmental temperature
		Weight	Per cent of snake's weight			
		<i>gm.</i>		<i>days hrs.</i>	<i>p. ct.</i>	<i>°C.</i>
Small Indian python.	Jan. 2-18, 1917....	454	8	?	100	17.6
	Nov. 6-14, 1916....	454	8	3 6	261	21.8
	Nov. 20-29 1916....	340	6	1 5	207	22.4
	Dec. 7-10, 1916....	397	7	2 5	214	22.1
	Feb. 5-10, 1917....	425	7	23	270	28.4
	Feb. 27-Mar. 1, 1917	454	8	22	105	37.1
	Mar. 10-15, 1916....	765	11	2 2	<sup>2</sup> 644	28.0
	July 19-27, 1916....	907	15	1 17	240	27.6
Boa B.....	Apr. 9-20, 1916....	<sup>3</sup> 397	3	2 12	147	28.1
Boa F.....	Mar. 15-17, 1917....	?	?	3 12	265	16.5
	Mar. 26-31, 1917....	595	11	1 3	198	32.0
	May 2-12, 1917....	539	9	3 9	ca. 195	24.1
Boa I.....	Apr. 25-May 12, 1917	425	7	?	100-200	18.3
	May 26-30, 1917....	284	5	23	232	29.2
	June 18-22, 1917....	510	8	1 6	209	32.8
	June 26-30, 1917....	454	8	1 17	250	28.8
Boa J.....	Oct. 7-11, 1919....	?	?	?	321	29.2
	Oct. 11-15, 1919....	<sup>4</sup> 142	3	1 15	....	29.2
	Oct. 26-31, 1919....	<sup>4</sup> 255	7	1 8	270	29.6
	Nov. 6-12, 1919....	<sup>4</sup> 340	9	1 15	365	29.3
Boa K.....	Aug. 4- 9, 1919....	<sup>4</sup> 1077	29	2 0	344	29.4
Gopher snake A....	{Sept. 5- 7, 1919....	<sup>5</sup> ?	?	1 7	....	29.1
	{Sept. 11-18, 1919....	<sup>4</sup> 142	5	14	169	29.3
Gopher snake B....	{Sept. 23-25, 1919....	<sup>4</sup> 142	7	17	271	29.3
	{Oct. 3- 5, 1919....	<sup>4</sup> 99	5	?	?	29.7
1931 python.....	Jan. 27-Feb. 3, 1931.	<sup>4</sup> 1191	22	2 18	606	31.6

<sup>1</sup> Rabbit unless otherwise specified. <sup>2</sup> Includes effect of prolonged fasting.

<sup>3</sup> Pigeon. <sup>4</sup> Guinea-pig. <sup>5</sup> Three sparrows.

purposes of comparison, in general one may consider that the food value was approximately proportional to the body weight.

It will be recalled that the increase in metabolism found with warm-blooded animals when fed protein usually is, at the maximum, 40 per cent. The invariably higher increase noted with snakes is striking. The lowest increment noted was 100 per cent in the experiment of January 2 to 18 with the small Indian python and the highest was 644 per cent in the experiment of March 10 to 15 with this same snake. The latter percentage value is probably complicated somewhat by the fact that the baseline was affected by prolonged fasting. The next highest increment, 606 per cent with the 1931 python, can not be complicated by prolonged

fasting, since the animal was fed in New York but three weeks before. This reaction to protein was a peak effect, but a peak lasting for at least some hours, thus accentuating the great effect of the ingestion of protein on the metabolism of these cold-blooded animals. The possibilities in further study are apparent.

#### COST OF DIGESTION OF PROTEIN WITH SNAKES

From these digestion experiments it is clear that the ingestion of protein in the form of a rabbit or guinea-pig results in a marked increase in the snake's metabolism. In several instances the heat production was studied after protein ingestion until it returned exactly or very closely to the measured or assumed predigestive baseline, and in these instances it is possible to determine the total increase in metabolism above the baseline resulting from the stimulus of the food. From the known weight of rabbit eaten and from an analysis of the composition of rabbit flesh made at the Nutrition Laboratory, the total calories consumed can be computed. Division of the total excess calories produced by the snake above its needs under standard conditions by the total calories consumed shows what percentage of the energy value of the food is expended in increased heat production. This percentage represents the stimulus or the cost of digestion due to  $x$  grams of protein and  $y$  grams of fat in the rabbit. Is there any relation between the caloric value of the ingested food and the increased heat production resulting from the stimulus to metabolism of the food ingested? The curves obtained for those digestive cycles during which the measurements were continued long enough for the metabolism to return to the baseline should throw considerable light upon the stimulus of ingested protein at different cell temperatures, knowledge concerning which is at present lacking. If the specific dynamic action of protein is known with the snake, one can compare it with that already determined with a warm-blooded animal, such as man, to discover whether the stimulus of protein is any greater or less with the snake than with man. To be sure, the amount of protein eaten by the snake was relatively large in proportion to its body weight. A half kilogram rabbit, for example, might correspond to nearly 5 per cent of the body weight of the snake that ate it. If the average man ate at one meal an amount of protein corresponding to 5 per cent of his body weight, he would consume about 8 pounds (3.6 kg.) of moderately fat flesh, an inconceivable situation exemplified perhaps only among the Eskimos studied by Krogh and Krogh.<sup>1</sup>

We have attempted to compute the specific dynamic action of protein in the case of the small Indian python, which was studied during three different digestive cycles at 22° C. The curves for these experiments have been shown in figure 73 (p. 268), together with a smoothed curve indicating the general average trend of the metabolism at this temperature. The average baseline for these three experiments has been accepted as 2.0 calories. The area between the horizontal line at 2 calories and the gen-

<sup>1</sup> Krogh, A., and M. Krogh, *A Study of the Diet and Metabolism of Eskimos*, Meddelelser om Grönland, 1913, 51, p. 1.

eral smoothed curve, which represents the excess heat production resulting from the protein ingestion, has been measured and converted into total calories, on the basis that (as shown by the scales for the ordinates and abscissæ in figure 73) each 1.2 square inches<sup>1</sup> are equivalent to 2.0 calories per kilogram of body weight per 24 hours. Each square inch would thus be equal to 1.7 calories per kilogram of weight. Since the average weight of the python in these three experiments was 6.31 kg.,<sup>2</sup> the total calories represented by each square inch would be 1.7 times 6.31 or 10.7 calories. The area represented by the general smoothed curve in figure 73, on the arbitrary assumption that the metabolism has returned to the baseline at the end of 6 days and 16 hours (which, as a matter of fact, it has not) measures 8.39 square inches. Multiplication of 8.39 by 10.7 gives 90 calories as the excess calories above the baseline.

The next step is to calculate the total calories ingested. Although doubtless in the literature there are a number of analyses of rabbit flesh and probably of adult animals, with these calculations in mind we analyzed the body of one rabbit typical of those fed to the snakes in these digestion experiments. The analysis of rabbit's flesh alone does not help much, however, because the snake digests the bones as well as the flesh, and only the pads of the feet and the hair are not actually destroyed by the digestive juices of the snake. The results of our one analysis of a rabbit are as follows:

	<i>Fresh weight in grams</i>
Live weight of rabbit.....	516
Blood that flowed out after killing.....	2.59
Hide and hair.....	54.53
Entire carcass, without hide and hair.....	449.72

The hide was cut into strips and a fresh portion analyzed. The nitrogen in the hide was 5.89 per cent, or a total of 3.21 grams. The carcass without hide and hair (but including blood and bones) was partially dried to 101.69 grams and the nitrogen in this amount was found to be 9.88 per cent. The total nitrogen in the carcass was thus 10.05 grams, and the total amount of nitrogen in the rabbit was 13.26 grams. No apportionment was made between the hide, the hair, and the claws, but probably

<sup>1</sup> Data for these digestion experiments were plotted on paper ruled in square inches. The distance between each two ordinates as shown in digestion charts reproduced in this report was, before reduction, exactly one inch, but distance between each two abscissæ representing days after eating was, for convenience in plotting, not one inch but 1.2 inches, so that each tenth of an inch as ruled on charting paper indicated two hours. Calculation of excess calories above baseline was made by planimetry area between horizontal baseline and curve for digestion experiment on unreduced chart, as plotted on square-inch paper, and planimetry area has been expressed as square inches. In reproduction of these charts, however, inch distances along horizontal base of each chart have not been indicated. Hence projections of ordinates and abscissæ across face of reduced reproductions of charts would not give square inches.

<sup>2</sup> In this calculation and subsequent calculations of excess calories produced, initial weight of snake at start of digestion experiment (which includes the weight of food) has been used as sufficiently accurate for the purpose. Necessary assumptions for baselines do not warrant any attempt at great refinement in method of using body weight data.

not more than half of these was undigestible and the total digestible nitrogen amounted to at least 11.5 grams.

The average body weight of the python in these three digestion experiments at 22° C. was 6.31 kg. and the average weight of the rabbits eaten was 397 grams, or 7 per cent of the snake's initial weight (corrected for weight of food). According to our analysis, a 500-gram rabbit would contain 11.5 grams of digestible protein. This python therefore received in a 400-gram rabbit as much nitrogen as a man might easily consume in his day's food. The fresh weight of the rabbit's carcass that was analyzed weighed 450 grams. The partially dried weight was 102 grams, or 23 per cent of the fresh weight. On the assumption that there was 10 per cent of water in the partially dried carcass, there would be approximately 90 grams of dry matter. Ninety grams of dry matter would represent 17 per cent of the live weight of the rabbit. The percentage of fat in the rabbit was not determined, but if it is assumed that the rabbit's flesh had an energy value of 5 calories per gram of dry matter, which is certainly a liberal amount, the digestible amount ingested would contain about 500 total calories. Probably in the experiments at 22° C. the calories ingested would be somewhat nearer 400 than 500, for the rabbits weighed on the average 397 and not 516 grams.

The increase in metabolism in excess of the baseline of 2 calories per kilogram of body weight per 24 hours as a result of the ingestion of 400 calories in the form of a rabbit was 90 calories, as has already been shown. The increase in heat production or the cost of digestion, so to speak, of the rabbit eaten therefore was 23 per cent of the total calories ingested, an increment considerably lower than that commonly found with warm-blooded animals.

If the baseline were considered to be 1.8 calories (the average for the experiments of November 6 to 14 and December 7 to 10, which were continued much longer than the experiment of November 20 to 29) the excess calories for 6½ days would be greater by 13 calories than that calculated above the 2-calorie level, and the specific dynamic action of the protein would thus be 26 per cent. It is to be recognized, however, that in this calculation no account has been taken of the sustained high level of metabolism above the baseline at about 2.6 calories between 6½ and 9½ days after food, with no indication of a return to the baseline on the ninth day. If the effect of digestion held over beyond 6½ days and the baseline were 1.8 instead of 2 calories, the excess calories resulting from the ingestion of the food would be greater than here estimated. But this point has not been taken into consideration in this first calculation. This brings out immediately one of the difficulties in attempting to compute the cost of digestion of food with the cold-blooded animal and leads again to the conclusion already drawn from our analysis of the protein experiments with the different snakes, namely, that the characteristic feature of the ingestion of rabbit flesh by snakes is a tendency for two phases in the digestive processes—one an increase in metabolism or a peak effect followed by a rapid decrease; and second, a metabolism sustained at a level above the baseline after the more active processes of digestion have



apparently ceased, probably in large part accounted for by deposited material, including protein. It can be seen, for example, that if the smoothed curve in figure 73 had been continued at a level of 2.6 calories to the end of the digestion experiments, *i.e.*, until about the end of the ninth day, the total excess calories would be considerably greater than those estimated above for 6½ days. Even at the end of 9 days, however, the experiment had not been continued long enough for the metabolism to return to the baseline, and we have every reason to believe that the higher level of metabolism was sustained for a considerable, although unknown, length of time. The estimate given above of 23 per cent for the specific dynamic action of protein is therefore a minimum figure.

Obviously the ideal experiment with any snake would be one in which the baseline was established at the start, when the nutritive state of the snake was not notably poor. The snake would then be given an animal of known weight and composition, determined by analysis of a similar animal of the same size, and the metabolism would be measured day after day until the baseline was again reached. Unfortunately it was impracticable to attempt to secure this ideal condition.

With boa F in the protein experiment of March 26 to 31 at 32° C. the assumed baseline is 3.54 calories and the metabolism toward the end of the experiment reached a level of about 4 calories. If we consider that the metabolism returned to the predigestive level in 2 days and 22 hours and accept the baseline as 4 calories, we find that the area included between this baseline and the curve equals 5.47 square inches. Since each 1.2 square inches are equivalent to 2.0 calories per kilogram of body weight per 24 hours and since boa F weighed in this experiment 6 kg., each square inch represents 10 total calories and 5.47 square inches represent 55 calories. A 595-gram rabbit had been eaten, for which we may assume an energy value of approximately 1 calorie per gram of flesh. The increased heat production at 32° or the cost of digestion of the protein therefore was 9 per cent of the energy value of the ingested protein, or less than half that noted with the python at 22° C.

In the protein experiment of May 2 to 12 at 24° C. with boa F, the course of the metabolism is well enough established to permit the calculation of the excess calories produced as a result of the ingestion of a 539-gram rabbit. In this experiment, as in the March experiment, the rabbit eaten represented, in proportion to the body weight of the snake, a meal with a large nitrogen content when compared with the meal of a human. The baseline for this May experiment, as actually determined just prior to the digestive cycle, was 1.15 calories. Since the postdigestive metabolism did not return to this level and the experiment was not continued long enough for the metabolism to reach this level, we are inclined to believe that the true baseline for this digestive cycle would be nearer 2 than 1.15 calories. There is, however, an enormous difference between these values, 2 calories being 80 per cent greater than 1.15 calories. In any method of calculating the excess heat production caused by the ingestion of food, this difference in baseline will play a large rôle. But since, after the maximum increase was attained, the metabolism steadily decreased for the three days and then reached a level below which it did not materially

change for the next four days, it can hardly be conceived that the after-effect of digestion continued at such a slow rate for so long a time. We are therefore considering, for purposes of rough calculation, that the baseline was really 2 calories.

The area between the baseline of 2 calories and the curve for the experiment of May 2 to 12 up to the end of 5 days and 20 hours equals 6.51 square inches, and the excess heat production has been computed to be 69 calories. The energy value of the rabbit would be about 540 calories and the excess heat production would therefore represent 13 per cent of this. The specific dynamic action of protein in this instance was somewhat greater than that found in the March experiment, although the environmental temperature was 24° in the May experiment and 32° C. in the March experiment, and the weight of the rabbit was somewhat greater in the March experiment. On the average, the specific dynamic action of protein with boa F was only about half that noted with the python at 22° C.

With boa J the total excess calories produced as a result of the ingestion of protein can be approximated for two experiments at about 29° C., in which, in striking contrast to most of the experiments after feeding with serpents, the metabolism returned to the predigestive baseline. Thus, during the digestive cycle of October 26 to 31, following the ingestion of a 255-gram guinea-pig and when the snake weighed 4.18 kg., the total excess heat production amounted to 52 calories. On the assumption that the energy value of the guinea-pig was 1 calorie per gram of flesh weight, the total calories ingested would be 255. The excess heat production therefore represents 20 per cent of the total calories ingested. In a second experiment on November 6 to 12 a much larger guinea-pig, weighing 340 grams, was eaten. The excess heat produced during this digestive cycle amounted to 66 calories or 19 per cent of the ingested calories.

With gopher snake A in the protein experiment of September 11 to 18 at 29° C. the postdigestive metabolism returned to essentially the initial baseline. The excess heat production amounted to 37 calories and the caloric intake (142-gram guinea-pig) to approximately 140 calories. The increment in heat production therefore was equivalent to 26 per cent of the total energy intake.

#### GENERAL CONCLUSIONS REGARDING COST OF DIGESTION OF PROTEIN WITH SNAKES

In these calculations of the cost of digestion of protein it must be recognized that two types of food are represented, the rabbit and the guinea-pig, that undoubtedly there were differences in the body composition of these animals that have not been allowed for in our calculations, and that the exact caloric intake in each instance is not known. Furthermore, in some cases the return of the metabolism to the predigestive baseline was not absolutely fixed and the baseline was not always ideally determined. With these reservations in mind, a comparison may be made of the percentage relationship between the excess calories produced and estimated calories in the intake or the cost of digestion, as shown in table 86.

With the exception of the experiment with boa F at 32° C., the cost of digestion of protein averages 20 per cent. This is much lower than the figure commonly assumed for man of 40 per cent and for the dog of 30 per cent. The return of the metabolism to the baseline in these protein digestion experiments with snakes was, however, the exception and not the rule. In most cases the heat production did not return to the initial level and there is a suggestion of a second phase of digestive activity represented by a metabolic level somewhat above the predigestive baseline. It is believed, however, that the experiments are of value in that they enable at least a rough comparison of the cost of digestion of protein with the cold-blooded animal and with man. Furthermore, the results may be directly compared in most instances with the observations during the fat digestion experiments, which will be considered next.

TABLE 86—*Cost of digestion of protein with snakes*

Snake	Date of digestion experiment	Environmental temperature	Weight of food as per cent of snake's weight	Calories in food	Excess calories produced above baseline	Cost of digestion of protein
		°C.	p. ct.			p. ct.
Python.....	3 expts.	22.0	7	400	90	23
Boa F.....	Mar. 26-31	32.0	11	595	55	9
Boa F.....	May 2-12	24.1	9	540	69	13
Boa J.....	Oct. 26-31	29.6	7	255	52	20
Boa J.....	Nov. 6-12	29.3	9	340	66	19
Gopher snake A.	Sept. 11-18	29.3	5	140	37	26

Although the evidence is incomplete, the experiments made with the python at 22° C. showed that the stimulus due to protein was essentially the same as that noted on the average with boa J and gopher snake A at 29° C. It was pointed out, however, in discussing the experiments with the python at 22° C., that the metabolism had not returned to the baseline at the end of the experiments, although it was approximating it. If the excess calories were to be increased to take into account the prolonged effect of digestion, this would result in a larger percentage value for the cost of digestion with the python. In all probability it may be concluded that the excess heat production caused by the ingestion of protein is with snakes practically independent of the temperature at which the digestion takes place. The digestive processes in the experiments at the low temperatures around 18° were so slow that the metabolism did not return to the baseline even when the expense was incurred of prolonging the experiment an unusual length of time. Hence at the low temperatures it has been impracticable to quantitate the excess calories. It will be recalled that a few protein experiments were made at low temperatures and that sometimes the snake disgorged the food. At other times there was evidence that it was distinctly injurious to attempt to feed the snake at low temperatures. Snakes do not normally live or digest food at temperatures much below 20° C.,<sup>1</sup> and hence it is a question whether in digestion

<sup>1</sup> See page 409 for discussion of very low respiratory quotients at 18°.

experiments made below 20° the snake would not be approaching a state of stupor which is rapidly reached at temperatures of 15° or 10° C. For this reason and because most of the experiments made by other investigators on cold-blooded animals have been carried out at fairly low temperatures, we felt that we ought in particular to study the snake at higher temperatures, although not failing to make observations for comparison at the lower temperatures.

It is conceivable that the size of the meal in proportion to the body weight of the snake may have some influence upon the degree to which the metabolism is stimulated by the ingestion of protein. In order to make this comparison, we have incorporated in table 86 values showing the percentage of the snake's body weight represented by the food intake. From this standpoint the smallest meal was eaten by the gopher snake and the largest by boa F in the experiment at 32° C., and the specific dynamic action of the protein was greatest with the smallest meal and least with the largest. Thus it would seem that there is some approximate correlation between the relative size of the meal eaten and the cost of digestion.

The tendency of these snakes after feeding to reach a plateau in metabolism measurably higher than the baseline suggests the importance of the deposit of both protein and fat accompanying the ingestion of these very large meals. Among the warm-blooded animals that we have studied, not even the goose or the pig can store as rapidly such large amounts of material as does the snake. The goose and the hog probably deposit greater amounts of fat, formed from the excess carbohydrate that they eat. The snake does not eat carbohydrate material and, as we shall soon see (p. 320), does not tolerate excessive amounts of fat. It would appear, therefore, as if the cold-blooded animal, especially the snake, is capable of much more rapid and relatively larger depositions of protein and fat than are any warm-blooded animals. Further studies of the nature and intensity of metabolic activity following these deposits are most desirable.

#### METABOLISM OF SNAKES DURING DIGESTION OF FAT

In all the protein experiments, the snakes voluntarily took the food offered them, usually rabbits or guinea-pigs, occasionally a pigeon or sparrow. To supplement our meager knowledge of the effect of the digestion of fat with humans or mammals, it seemed desirable to feed some of the snakes forcibly with a relatively large amount of beef fat<sup>1</sup> and then note the effect upon the digestive activity. The feeding habits of serpents have been extensively studied by Ditmars,<sup>2</sup> and the art of forced feeding of snakes, particularly the large boas, has been most accurately developed by Ditmars and his associates. His unique personal experience in such

<sup>1</sup>In view of the large masses of undigested fat excreted by the snakes that were thus fed, it is highly probable that a fat with a lower melting point should have been selected. This would be particularly important in experiments in which the snake was maintained at a low temperature.

<sup>2</sup>Ditmars, R. L., *Zoologica*, 1912, **1**, p. 197. F. W. FitzSimons (*Pythons and Their Ways*, London, 1930, p. 20) also discusses the method of forced feeding of serpents and their feeding in captivity.

forced feeding was of incalculable service to us, and as a result the technical side of the problem presented no great difficulties.

#### Boa G

The first experiment with fat was made with boa G on May 16 to 30 at an average temperature of 29.4° C. The standard carbon-dioxide production had been measured on May 14 to 16 at 28.1°, but when corrected to 29.4° according to the percentage increase in metabolism with increasing temperature (22 per cent per degree increase between 20° and 30°) as indicated by the curve for all boas in figure 54, it was found to be 0.743 gram, equivalent to 2.48 calories. These values have therefore been used to represent the predigestive baseline. On May 16, boa G was fed 227 grams of beef fat wrapped in a rabbit pelt weighing 57 grams. The body weight of boa G at the start of the digestion experiment includes (as is the case with all the other snakes in both the protein and the fat series) the weight of the food. If the body weight is corrected for the food eaten, the total weight of the fat and pelt fed to boa G represents 3 per cent of its actual weight. It had not eaten for about 24 days. The results are recorded in table 87. The carbon-dioxide production instantly increased greatly and then fell again rapidly in the first few hours. This undoubtedly is a reflection of the effect of the rather severe handling and the insult due to the forced feeding. The production of carbon dioxide quickly reached a level of about 1.2 grams and fluctuated above and below this value during the rest of the experiment, practically 13 days. Even at the end of the experiment it was nearly twice the assumed baseline.

The results of this experiment, expressed in calories per kilogram of body weight per 24 hours, have been plotted in figure 80 (the lowest curve), referred to the time after eating. Here the picture is clear of a constant, sustained metabolism of about 4.2 calories throughout almost the entire 13 days. Since the baseline for this experiment was 2.48 calories, there was an increase on the average of 69 per cent in the metabolism continuing for 13 days. Part of this increase undoubtedly must be attributed to the stimulus resulting from the ingestion of the rabbit pelt. The analysis of the rabbit made by the Nutrition Laboratory (see page 300) showed that the hide and hair (weighing 55 grams or practically the same as the rabbit pelt fed to boa G in this May experiment) contained 3.21 grams of nitrogen. It may be assumed that approximately half of this amount, or 1.6 grams, was digested. This amount of protein by itself, without the fat, would stimulate the metabolism to some degree, but it is hardly likely that the stimulus would persist for any great length of time after the first day or two, especially at the high temperature of 29° C. The elevated level of the metabolism, sustained through the thirteenth day, is therefore attributable in large part to the ingestion of the fat. In any event, if the baseline is assumed to be a logical one, there was a sustained increase in metabolism of 69 per cent continuing for 13 days, due primarily to the ingestion of fat. It is regretted that the experiment could not have been continued until the baseline was again reached.

Although this May experiment continued for 46 periods, when the respiration chamber was opened, it was found that boa G had shed its skin.

TABLE 87—*Metabolism of boa G during fat digestion*  
(29.4° C.; 227 gm. beef fat and 57 gm. rabbit  
pelt fed May 16)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1918	<i>days hrs.</i>		<i>gm.</i>	<i>cal.</i>
<u>May 14-16</u>	<u>22</u>	.....	<sup>2</sup> 0.743	<sup>2</sup> 2.48
May 16	2	1	1.856	6.19
	4	2	1.287	4.29
May 16-17	6	3	.984	3.28
May 17	11	4	.927	3.09
	16	5	1.069	3.56
	22	6	1.190	3.97
May 17-18	1 5	7	.978	3.26
May 18	1 13	8	1.236	4.12
	1 17	9	1.365	4.55
	1 20	10	1.172	3.91
	1 23	11	1.259	4.20
May 18-19	2 3	12	1.173	3.91
May 19	2 10	13	1.159	3.86
	2 20	14	1.270	4.23
May 19-20	3 2	15	1.379	4.60
May 20	3 10	16	1.245	4.15
	3 16	17	1.456	4.85
	3 22	18	1.335	4.45
May 20-21	4 5	19	1.285	4.28
May 21	4 13	20	1.395	4.65
	4 21	21	1.267	4.22
May 21-22	5 5	22	1.235	4.12
May 22	5 14	23	1.382	4.61
	5 21	24	1.416	4.72
May 22-23	6 3	25	1.275	4.25
May 23	6 10	26	1.229	4.10
	6 19	27	1.449	4.83
May 23-24	7 1	28	1.320	4.40
May 24	7 7	29	1.136	3.79
	7 14	30	1.407	4.69
	7 22	31	1.354	4.51
May 24-25	8 5	32	1.171	3.90
May 25	8 14	33	1.440	4.80
	8 22	34	1.173	3.91
May 25-26	9 5	35	1.150	3.83
May 26	9 13	36	1.273	4.24
	9 21	37	1.270	4.23
May 26-27	10 3	38	1.480	4.93
May 27	10 10	39	1.208	4.03
	10 19	40	1.213	4.04
May 27-28	11 4	41	1.241	4.14
May 28	11 17	42	1.161	3.87
May 28-29	12 1	43	1.151	3.84
May 29	12 12	44	1.211	4.04
	12 21	45	1.248	4.16
May 30	13 7	46	1.225	4.08

<sup>1</sup> Snake weighed 8.33 kg. on May 13, and 8.62 kg. (including food) on May 16. Weight assumed to have decreased to 8.43 kg. in periods 45 and 46. Weighed 8.42 kg., including shedded skin, on May 30, after removal from respiration chamber. Weight minus shedded skin was 8.36 kg.

<sup>2</sup> Corrected to 29.4° C.

There were no fatty feces, however. The skin, while still moist, weighed 57 grams. The actual time when the skin was shed is not known.

In the second experiment with boa G, 340 grams of beef fat were wrapped in a rabbit pelt, weighing 43 grams, and forced down the throat of the animal. This meal represented 5 per cent of the snake's initial weight (deducting the weight of food). The observations began on June 12, 15 minutes after the fat was given, and continued through June 25. Boa

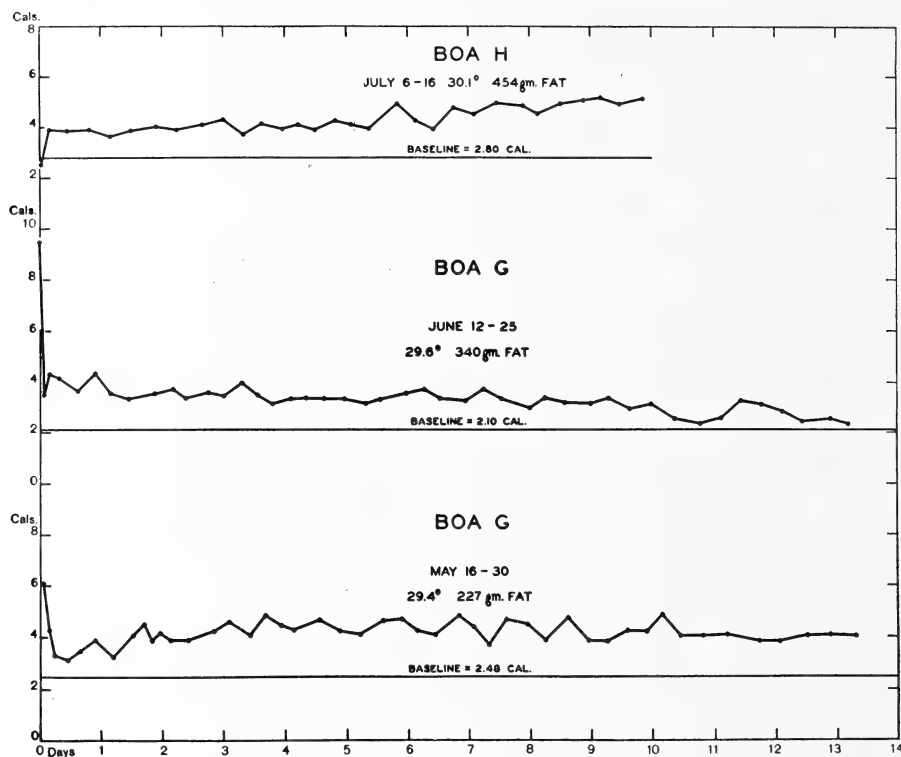


FIG. 80—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER FAT INGESTION—BOAS G AND H.

Date of digestion experiment, average environmental temperature during experiment, and amount of fat fed to snake are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve.

G had not previously been fed since May 16, or for 27 days. A baseline had been established for boa G on June 8-9 at 29.1°, practically the same temperature as that of the June digestion experiment. At that time the standard carbon-dioxide production was 0.631 gram and the heat production 2.10 calories. Boa G was returned to the reptile house on June 9, following the standard metabolism experiment, but was brought back to the laboratory and put into the respiration chamber again at 2 p.m., June 10. For 15 minutes on June 12 the boa was out of the respiration chamber, in which it had been at a temperature of about 30° C., and was in the room

TABLE 88—*Metabolism of boa G during fat digestion*  
(29.6° C.; 340 gm. beef fat and 43 gm. rabbit  
pelt fed June 12)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1918 June 8-9	days hrs. 22	.....	gm. 0.631	cal. 2.10
June 12	15 mins.	1	2.827	9.42
		2	1.031	3.44
		3	1.289	4.30
June 12-13	8	4	1.249	4.16
June 13	15	5	1.081	3.60
	22	6	1.303	4.34
	1 4	7	1.052	3.51
June 13-14	1 11	8	.999	3.33
June 14	1 21	9	1.055	3.52
	2 4	10	1.091	3.64
June 14-15	2 9	11	1.014	3.38
June 15	2 18	12	1.078	3.59
	3 0	13	1.021	3.40
	3 7	14	1.172	3.91
June 15-16	3 13	15	1.022	3.41
June 16	3 19	16	.941	3.14
	4 2	17	.998	3.33
June 16-17	4 8	18	1.014	3.38
June 17	4 15	19	.998	3.33
	4 23	20	.995	3.32
June 17-18	5 7	21	.952	3.17
June 18	5 13	22	.974	3.25
	5 23	23	1.054	3.51
	6 6	24	1.093	3.64
June 18-19	6 12	25	.990	3.30
June 19	6 22	26	.963	3.21
	7 5	27	1.096	3.65
June 19-20	7 12	28	.984	3.28
June 20	7 23	29	.888	2.96
	8 5	30	1.008	3.36
June 20-21	8 13	31	.950	3.17
June 21	8 23	32	.936	3.12
June 21-22	9 6	33	1.006	3.35
June 22	9 14	34	.878	2.93
	9 23	35	.927	3.09
June 22-23	10 8	36	.776	2.59
June 23	10 18	37	.700	2.33
	11 2	38	.776	2.59
June 23-24	11 10	39	.966	3.22
June 24	11 18	40	.921	3.07
	12 2	41	.840	2.80
June 24-25	12 10	42	.724	2.41
June 25	12 21	43	.769	2.56
	13 4	44	.706	2.35

<sup>1</sup> Snake weighed 8.32 kg. on June 9 and 8.38 kg. (including food) on June 12. Weight assumed to have decreased to 8.07 kg. in periods 43 and 44. Weighed 8.05 kg. on June 26.



at about 20° C., while it was being forcibly fed. The results of this experiment are recorded in table 88 and in the middle curve in figure 80.

Immediately after the feeding there was a great increase in carbon-dioxide production to 2.827 grams, which undoubtedly reflected in large part the great struggle and the insult resulting from the forced feeding. The production decreased in the second period to a little over one gram, and thereafter through the thirty-third period it remained at about one gram. It then decreased further, but at no time reached the baseline of 0.631 gram.

The middle curve in figure 80 representing this experiment of June 12 to 25 shows the great increase in heat production to 9.42 calories that occurred immediately after the feeding, the subsequent immediate decrease to a level of about 3.8 calories or 80 per cent above the baseline of 2.10 calories, and the tendency for the heat production to fall off slowly toward the end of the experiment. This baseline was nearly reached by the tenth or eleventh day. During the experiment itself, 170 grams of feces were passed. These were very greasy, showing that a considerable proportion of the fat had not been digested. Boa G at 29.6° C. thus gave evidence of a stimulated metabolism due to fat ingestion continuing for a long period, with an absence of a peak such as was found with protein.

The rectal temperature of boa G immediately after the experiment, on June 25, was 29.41°, when the temperature of the respiration chamber was 29.0° and that of the room 20.4° C.

#### BOA H

Another boa to be subjected to a study of the effect of digestion of fat was boa H, which weighed essentially 7 kg. The fat digestion experiment was made from July 6 to 16 at an average temperature of 30° C. A standard metabolism experiment on June 3-4 gave a value for heat production at about 30° C. agreeing well, on the average, with the general curve for all boas in figure 54. Hence for the baseline it may be considered that the carbon-dioxide production at 30° was 0.84 gram and the heat production 2.80 calories. The boa was fed 454 grams of beef fat in a rabbit pelt weighing 42 grams. Presumably the boa had not been fed for 43 days before. The low carbon-dioxide production in the first period of the digestion experiment (table 89) may be due to the fact that boa H was out of the respiration chamber for from 20 to 25 minutes while the feeding was going on, and unquestionably the temperature of the room was not 30° C. The low value may also possibly be explained by the fact that less than 1 gram of carbon dioxide was collected and weighed during this period, and any error in weighing would therefore play a relatively large rôle. After the first period the carbon-dioxide production increased to a level of about 1.1 or 1.2 grams, at which it remained until the nineteenth period, when it gradually became greater, with a tendency to rise at the time the experiment was concluded. For the greater part of the time, therefore, the carbon-dioxide production was almost double the baseline, with no evidence of a peak. Boa H weighed 7 kg., and hence the amount of food given was an appreciable proportion (8 per cent) of its own weight.

The graphic representation of the course of the metabolism during this fat experiment with boa H is given in the uppermost curve in figure 80. The baseline, taken from the curve for all boas at 30° C., is considered to be 2.80 calories. After the fat ingestion, for the first half of the experi-

TABLE 89—*Metabolism of boa H during fat digestion*  
(30.1° C.; 454 gm. beef fat and 42 gm. rabbit  
pelt fed July 6)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1918	days hrs.		gm. 20.84	cal. 22.80
July 6	1	1	.769	2.56
July 6-7	4	2	1.151	3.84
July 7	11	3	1.143	3.81
	20	4	1.154	3.85
July 7-8	1 4	5	1.083	3.61
July 8	1 12	6	1.145	3.82
	1 22	7	1.201	4.00
July 8-9	2 6	8	1.180	3.93
July 9	2 16	9	1.222	4.07
	3 0	10	1.280	4.27
July 9-10	3 8	11	1.116	3.72
July 10	3 15	12	1.254	4.18
	3 23	13	1.182	3.94
July 10-11	4 5	14	1.216	4.05
July 11	4 12	15	1.180	3.93
	4 20	16	1.269	4.23
	5 2	17	1.224	4.08
July 11-12	5 9	18	1.196	3.99
July 12	5 20	19	1.471	4.90
	6 3	20	1.267	4.22
July 13	6 10	21	1.192	3.97
	6 18	22	1.430	4.77
July 13-14	7 2	23	1.346	4.49
July 14	7 11	24	1.479	4.93
	7 21	25	1.440	4.80
July 14-15	8 3	26	1.365	4.55
July 15	8 12	27	1.481	4.94
	8 21	28	1.508	5.03
July 15-16	9 4	29	1.555	5.18
July 16	9 11	30	1.456	4.85
	9 20	31	1.543	5.14

<sup>1</sup> Snake weighed 6.97 kg. (including food) on July 6. Weight assumed to have decreased to 6.74 kg. in periods 28 to 31. Weighed 6.72 kg. sometime on July 16, after removal from respiration chamber.

<sup>2</sup> Based on curve in figure 54, page 224.

ment at least, the heat production remained at a level of practically 4 calories. Thereafter it averaged more nearly 4.6 calories. Thus throughout the entire experiment the metabolism of boa H was at a level 50 per cent or more above the baseline. The increase can be attributed only in small part to the nitrogen of the pelt, and is distinct evidence of the influence of fat ingestion upon the metabolism.

## Boa J

With boa J the first experiment (December 5), to determine the effect of the ingestion of beef fat was made at a much lower temperature ( $21^{\circ}$ ) than the observations with boas G and H, which were carried out at nearly  $30^{\circ}$  C. Prior to this, on December 1 to 5, the baseline had been determined at  $20.7^{\circ}$ , almost the same as that of the fat experiment, and the carbon-dioxide production was found to be 0.267 gram, equivalent to 0.89 calorie. On the afternoon of December 5 boa J was forcibly fed 198 grams of beef fat wrapped in a rabbit pelt weighing 29 grams, a total of 227 grams which represented 6 per cent of its initial weight (less food). It had not been fed previously for 20 days. About half an hour was required for the stuffing process, which took place at the ordinary temperature of the room. The boa was put back into the respiration chamber after the forced feeding, and the metabolism measurements began within an hour. The results are reported in table 90. In the first period the carbon-dioxide production was high, 1.315 grams, reflecting the effect of agitation due to the handling. In the second period it had decreased to 0.436 gram and thereafter tended to rise slowly. The boa was restless in the twenty-third period and there was accordingly a great increase (twofold) in the carbon-dioxide production during this period. Because of the animal's restlessness, the respiration chamber was opened at the end of the twenty-third period, and it was found that about 380 grams of feces had been passed, which were very fatty; indeed, a microscopic examination showed particles of fat that had undergone no change. Boa J was removed from the chamber, washed and dried, and put back into the chamber for three more periods. The snake was out of the chamber between periods 23 and 24 for about one hour. At the end of the entire experiment, that is, 17 days and 2 hours after the ingestion of the fat, the carbon-dioxide production was at a level of 0.552 gram, or somewhat more than twice the so-called baseline.

The results of this fat experiment of December 5 to 22 with boa J have been plotted in figure 81 (the lowest curve), expressed as calories and referred to time since eating. That portion of the curve represented as a broken line indicates the time when boa J was removed from the respiration chamber and feces were found. The baseline at 0.89 calorie is indicated by the horizontal line. It is seen from this curve that after the initial rise in heat production due to the feeding, the metabolism remained for the greater part of the time in the neighborhood of 1.8 or 1.9 calories, that is, 100 per cent above the measured baseline. The fact that this higher level was maintained even through the seventeenth day is indicative of the slowness in the digestive processes when fat has been ingested, particularly at a low temperature. Indeed, at the environmental temperature of  $21^{\circ}$  the snake's body temperature would not represent the melting point of beef fat, and the effect of the digestive processes upon the fat must have been extremely slow. Furthermore, it was noted from the feces collected that a considerable amount of the fat was actually excreted unchanged.

With boa J a second fat experiment was conducted somewhat later, from December 30 to January 10 (table 91). At the end of the first fat experiment, on December 23, the boa was taken to the reptile house, where its

average body temperature would be not far from 30° C. It remained there until December 26, when it was put into the respiration chamber, at about 32° C. A baseline value was obtained on December 27 to 29 at 30.8°, when the carbon-dioxide production averaged 1.132 grams. This, increased 22 per cent per degree increase in temperature, as explained on

TABLE 90—*Metabolism of boa J during fat digestion*  
(20.9° C.; 198 gm. beef fat and 29 gm. rabbit  
pelt fed Dec. 5)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919 Dec. 1-5	<i>days hrs.</i> 16	.....	<i>gm.</i> 0.267	<i>cal.</i> 0.89
Dec. 5-6	1	1	1.315	4.38
Dec. 6	9	2	.436	1.45
	20	3	.363	1.21
Dec. 6-7	1 7	4	.449	1.50
Dec. 7-8	1 19	5	.375	1.25
Dec. 8	2 10	6	.529	1.76
Dec. 8-9	3 1	7	.440	1.47
Dec. 9	3 14	8	.455	1.52
Dec. 9-10	4 2	9	.460	1.53
Dec. 10-11	4 16	10	.597	1.99
Dec. 11	5 9	11	.433	1.44
Dec. 11-12	5 21	12	.444	1.48
Dec. 12	6 9	13	.497	1.66
Dec. 12-13	7 0	14	.566	1.89
Dec. 13-14	7 17	15	.562	1.87
Dec. 14	8 9	16	.529	1.76
Dec. 14-15	9 2	17	.512	1.71
Dec. 15-16	10 0	18	.497	1.66
Dec. 16-17	10 15	19	.511	1.70
Dec. 17	11 9	20	.546	1.82
Dec. 17-18	12 2	21	.619	2.06
Dec. 18-19	12 22	22	.590	1.97
Dec. 19-20	13 18	23	<sup>2</sup> 1.171	<sup>2</sup> 3.90
Dec. 20-21	14 19	24	.622	2.07
Dec. 21-22	15 14	25	.724	2.41
Dec. 22	16 13	26	.552	1.84

<sup>1</sup> Snake weighed 4.09 kg. on Dec. 1, 4.32 kg. (including food) on Dec. 5, and 3.92 kg. on Dec. 20. Weight assumed to have been 4.32 kg. during first 23 periods and 3.92 kg. in periods 24 to 26.

<sup>2</sup> Restless in period 23. Chamber opened and feces found. Snake was taken out of chamber for about one hour between periods 23 and 24, to be cleaned.

page 251, to bring it to the actual temperature of the digestion experiment, 31.5° C., corresponds to 1.306 grams of carbon dioxide, representing 4.35 calories. These values are therefore used as the baseline for the fat experiment of December 30 to January 10.

Boa J was kept in the respiration chamber for a day following the baseline experiment of December 27 to 29. It was taken out to be weighed

and fed on the afternoon of December 30 and then returned to the chamber. It was fed 227 grams of beef fat and a 57-gram guinea-pig pelt, a total of 284 grams (actually 8 per cent of its body weight). Boa J had last been fed 25 days before, on December 5. Since the feeding of the snake was forced, there was considerable handling and agitation. This may explain in part the relatively high metabolism values obtained so soon after food, although in all probability the values for the first few periods are really somewhat low, due to the fact that the boa was cooled slightly when taken out into the room temperature and this cooling effect

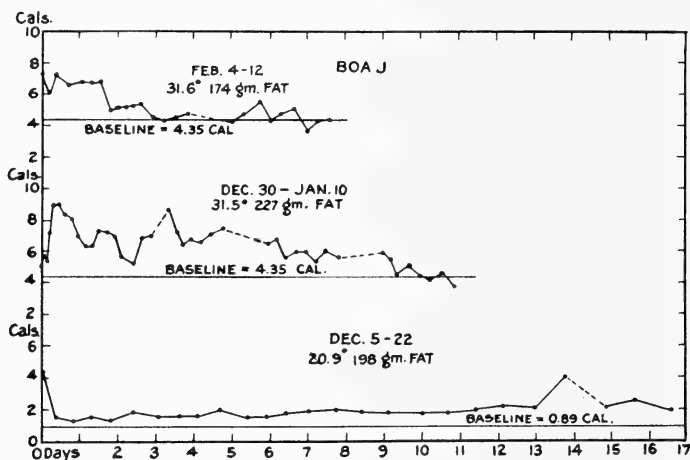


FIG. 81—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER FAT INGESTION—Boa J.

Date of digestion experiment, average environmental temperature during experiment, and amount of fat fed to snake are indicated on chart near particular curve to which data belong. *Standard* heat production per kilogram of body weight per 24 hours at same environmental temperature as that of digestion experiment is shown by "baseline" below curve. Those portions of curves shown as broken lines represent times when respiration chamber was opened to see if snake was all right.

was not wholly offset by the struggle. In any event the metabolism was high, and the peak occurred at about the eighth or eleventh hour, with another high value complicated by an increase in environmental temperature and activity 3 days and 8 hours after food. The respiration chamber was opened between periods 18 and 19 to see if the snake was all right, and again between periods 25 and 26 and periods 33 and 34, the snake, however, not being removed. It was found on the morning of January 8 that boa J had shed its skin, weighing 57 grams. The carbon-dioxide production decreased as the experiment progressed and in the last period, 10 days and 19 hours after food, it was 1.121 grams or below the assumed baseline. Boa J was returned to the reptile house on January 11. Here fatty feces were passed on January 12 and during the night of January 18-19. The boa swallowed three dead rats on January 12.

The picture is somewhat more clearly shown by the middle curve in figure 81. The sections of broken line indicate those times when the

TABLE 91—*Metabolism of boa J during fat digestion*  
(31.5° C.; 227 gm. beef fat and 57 gm. guinea-pig  
pelt fed Dec. 30)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1919-20 Dec. 27-29	<i>days hrs.</i> <u>22</u>	.....	<i>gm.</i> <u><sup>2</sup>1.306</u>	<i>cal.</i> <u><sup>4</sup>4.35</u>
Dec. 30	20 mins.	1	1.519	5.06
	2	2	1.694	5.65
	3	3	1.596	5.32
	5	4	2.104	7.01
Dec. 30-31	8	5	2.659	8.86
Dec. 31	11	6	2.676	8.92
	15	7	2.501	8.34
	19	8	2.401	8.00
	23	9	2.065	6.88
	1 3	10	1.884	6.28
Dec. 31-Jan. 1	1 8	11	1.873	6.24
Jan. 1	1 12	12	2.173	7.24
	1 17	13	2.142	7.14
	1 22	14	2.081	6.94
Jan. 1-2	2 2	15	1.689	5.63
Jan. 2	2 10	16	1.555	5.18
	2 15	17	2.039	6.80
	2 21	18	2.084	6.95
Jan. 2-3	3 8	<sup>3</sup> 19	2.558	8.53
Jan. 3	3 13	20	2.132	7.11
	3 17	21	1.930	6.43
	3 22	22	1.994	6.65
Jan. 3-4	4 4	23	1.943	6.48
Jan. 4	4 10	24	2.088	6.96
	4 18	25	2.195	7.31
Jan. 5	5 22	<sup>3</sup> 26	1.932	6.44
Jan. 5-6	6 4	27	2.003	6.68
Jan. 6	6 9	28	1.635	5.45
	6 16	29	1.790	5.97
	6 22	30	1.770	5.90
Jan. 6-7	7 4	31	1.573	5.24
Jan. 7	7 10	32	1.749	5.83
	7 18	33	1.666	5.55
Jan. 8	8 23	<sup>3</sup> 34	1.753	5.84
	9 3	35	1.626	5.42
Jan. 8-9	9 7	36	1.322	4.41
Jan. 9	9 15	37	1.488	4.96
	9 22	38	1.280	4.27
Jan. 9-10	10 4	39	1.228	4.09
Jan. 10	10 12	40	1.328	4.43
	10 19	41	1.121	3.74

<sup>1</sup> Snake weighed 3.64 kg. on Dec. 26, and 3.91 kg. (including food) on Dec. 30. Weight assumed to be 3.79 kg. in periods 38 to 41. Weighed 3.77 kg. on Jan 11.

<sup>2</sup> Corrected to 31.5° C.

<sup>3</sup> Chamber opened between periods 18 and 19, 25 and 26, and 33 and 34, to see if snake was all right. The snake was not removed from the chamber.

respiration chamber was opened. There is considerable irregularity in the curve, caused in part at least by the seemingly unavoidable changes in environmental temperature in two cases. Thus, in the period beginning 3 days and 8 hours after food the temperature went up at least 2 degrees, and likewise in the period 8 days and 23 hours after food. At the average temperature of 31.5° C. there were also high values on several occasions. But in general the excess metabolism can be considered as that above the baseline of 4.35 calories. There are apparently two peaks. One probably is explained by the increase of 2° in temperature and by activity. The other is the first suggestion of any real peak in metabolism with fat digestion. Seemingly the heat production of boa J tended to return to approximately the predigestive value. The considerable increase in the metabolism of this boa due to the ingestion of fat at 31.5° C. is striking evidence of a real effect ("specific dynamic action") of fat with these snakes.

The last fat experiment with boa J was on February 4 to 12, likewise at a high temperature, averaging 31.6° C. (table 92). The baseline was not determined directly before the experiment nor at any other time at 31.6° C. According to the curve for all boas, the probable heat production at 31.6° C. is 3.38 calories (fig. 54, p. 224). This differs from the determined value for boa J on December 27 to 29, which, when corrected to 31.5°, is 4.35 calories. In view of the tendency for boa J's metabolism to return to its baseline, we may anticipate the results of this particular experiment and note that a level of about 4 calories was reached at the end of the series of observations. Hence we feel justified in using the same baseline employed for the experiment of December 30 to January 10, that is, 1.306 grams of carbon dioxide or 4.35 calories.

Boa J was put into the respiration chamber at 2<sup>h</sup>30<sup>m</sup> p.m., February 3. It was removed to be fed at 3<sup>h</sup>30<sup>m</sup> p.m., February 4, and returned to the chamber an hour later. It was fed 174 grams of beef fat in a rabbit pelt, weighing in all 206 grams or 5 per cent of its weight. It had not been fed since January 12 or for 23 days. Between periods 17 and 18 the chamber was opened for a long interval, but the snake was not removed.

We attempted to hold the environmental temperature on the average at 31.6° C., but the first two periods were at a lower temperature, the first at 27.5° C. In spite of this fact, however, and in spite of the fact that the animal had been out in the room air for an hour, the agitation and insult of the forced feeding resulted in a great increase in the carbon-dioxide production to 2.161 grams in the first period. The carbon-dioxide production remained at a level of about 2 grams, or a little over, for 1 day and 13 hours. There was then a sudden, almost inexplicable fall, with again a plateau for a day, and then a further fall. Finally, on February 10 to 12, that is, on the sixth to the eighth days, the carbon-dioxide production was essentially the same as the baseline. Although there was no definite index of a peak in metabolism, the higher values during the first two days are noticeable. The picture is clearer in figure 81 (uppermost curve). There was a fairly considerable increase in metabolism for the first 2½ days or for nearly 3 days, and thereafter a tendency for

the metabolism to remain somewhat above the baseline of 4.35 calories. It therefore appears that with this particular snake the ingestion of fat produced a more rapid and momentarily more pronounced increase in metabolism than was the case with any of the other snakes thus far studied.

TABLE 92—*Metabolism of boa J during fat digestion*  
(31.6° C.; 174 gm. beef fat and 32 gm. rabbit  
pelt fed Feb. 4)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1920 Dec. 27-29	<i>days hrs.</i> 22	.....	<i>gm.</i> <sup>2</sup> 1.306	<i>cal.</i> <sup>3</sup> 4.35
Feb. 4	1	1	2.161	7.20
Feb. 4-5	5	2	1.811	6.04
Feb. 5	9	3	2.160	7.20
	17	4	1.949	6.50
	22	5	.....	.....
	1 1	6	2.038	6.79
Feb. 5-6	1 7	7	2.001	6.67
Feb. 6	1 13	8	2.035	6.78
	1 19	9	1.499	5.00
	2 0	10	1.548	5.16
Feb. 6-7	2 5	11	1.555	5.18
Feb. 7	2 9	12	1.568	5.23
	2 14	13	1.581	5.27
	2 21	14	1.350	4.50
Feb. 7-8	3 4	15	1.295	4.32
Feb. 8	3 12	16	1.348	4.49
	3 20	17	1.408	4.69
Feb. 9	4 23	<sup>3</sup> 18	1.298	4.33
Feb. 9-10	5 6	19	1.384	4.61
Feb. 10	5 17	20	1.655	5.52
	5 23	21	1.308	4.36
Feb. 10-11	6 6	22	1.390	4.63
Feb. 11	6 15	23	1.504	5.01
	6 23	24	1.116	3.72
Feb. 11-12	7 5	25	1.271	4.24
Feb. 12	7 13	26	1.305	4.35

<sup>1</sup>Snake weighed 3.64 kg. on Dec. 26, and 4.04 kg. (including food) on Feb. 4. Weight assumed to have decreased to 4.01 kg. in periods 21 to 26. Weighed 4.00 kg. on Feb. 12, after removal from respiration chamber.

<sup>2</sup>Corrected to 31.5° C.

<sup>3</sup>Chamber was opened between periods 17 and 18, but snake was not removed.

#### BOA M

With the 4-kg. boa M, a fat digestion experiment was carried out from January 13 to February 3 at an average environmental temperature of 21.9° C. On December 30 to January 2 a baseline experiment was made with this snake at 21.0°, in which it was found that the standard carbon-dioxide production was 0.491 gram and the heat production 1.64 calories.



If these values are corrected to 21.9° C., they become 0.588 gram of carbon dioxide and 1.96 calories. This corrected baseline is considerably

TABLE 93—*Metabolism of boa M during fat digestion*  
(21.9° C.; 198 gm. beef fat and 29 gm. rabbit  
pelt fed Jan. 13)

Date	Time since eating	Period	Per kg. <sup>1</sup> per 24 hours	
			Carbon dioxide	Heat produced
1920 Dec. 30-Jan. 2	<i>days hrs.</i> 24	.....	<i>gm.</i> °0.588	<i>cal.</i> °1.96
Jan. 13	1	1	.800	2.67
Jan. 13-14	4	2	.574	1.91
Jan. 14	11	3	.488	1.63
	18	4	.529	1.76
Jan. 14-15	1 4	5	.549	1.83
Jan. 15-16	1 19	6	.576	1.92
Jan. 16	2 11	7	.660	2.20
Jan. 16-17	3 3	8	.709	2.36
Jan. 17-18	3 20	9	.642	2.14
Jan. 18	4 10	10	.603	2.01
Jan. 18-19	5 6	11	.568	1.89
Jan. 19-20	5 22	12	.611	2.04
Jan. 20	6 10	13	.593	1.98
Jan. 20-21	7 3	14	.723	2.41
Jan. 21-22	7 18	15	.667	2.22
Jan. 22	8 11	16	.667	2.22
Jan. 22-23	9 3	17	.823	2.74
Jan. 23-24	9 20	18	.720	2.40
Jan. 24	10 11	19	.807	2.69
Jan. 24-25	11 3	20	.694	2.31
Jan. 25-26	11 20	21	.775	2.58
Jan. 26	12 11	22	.816	2.72
Jan. 26-27	13 3	23	.883	2.94
Jan. 27	13 22	°24	.506	1.69
Jan. 27-28	14 3	25	.935	3.12
Jan. 28-29	14 19	26	.735	2.45
Jan. 29	15 11	27	.744	2.48
Jan. 29-30	16 3	28	.660	2.20
Jan. 30-31	16 19	29	.762	2.54
Jan. 31	17 11	30	.714	2.38
Jan. 31-Feb. 1	18 3	31	.727	2.42
Feb. 1-2	18 20	32	.707	2.36
Feb. 2	19 11	33	.756	2.52
Feb. 2-3	20 3	34	.705	2.35

<sup>1</sup> Snake weighed 4.06 kg. on Dec. 29, 4.05 kg. (including food) on Jan. 13, and 3.83 kg. on Jan. 27. Weight assumed to have decreased to 3.85 kg. in period 23 and to 3.73 kg. in period 34. Weighed 3.71 kg. on Feb. 3, after removal from respiration chamber.

<sup>2</sup> Corrected to 21.9° C.

<sup>3</sup> There was an interruption of about 2½ hours between periods 23 and 24.

above that indicated by the curve for all boas, and it is clear that boa M had a characteristically high metabolism. At 2<sup>h</sup>30<sup>m</sup> p.m., January 13, boa M was forcibly fed 198 grams of fat wrapped in a rabbit pelt, in all 227 grams, equivalent to 6 per cent of its body weight. It had been fed

previously on December 23 and 25, but apparently all the food was disgorged on December 28. It had also been fed on December 5. The results of the digestion experiment are given in table 93. The carbon-dioxide production was high in the first period, following the handling and the agitation. In the second period it was slightly below the baseline, but thereafter it slowly increased through the twenty-third period, when the chamber was opened for about 2½ hours and a small amount of fatty feces removed. At this time it was noted that the snake was about to shed. On closing the chamber, the experiment continued for eleven more periods. The total duration of the experiment was 20 days and 21 hours, the longest experiment made in either the protein or the fat series.

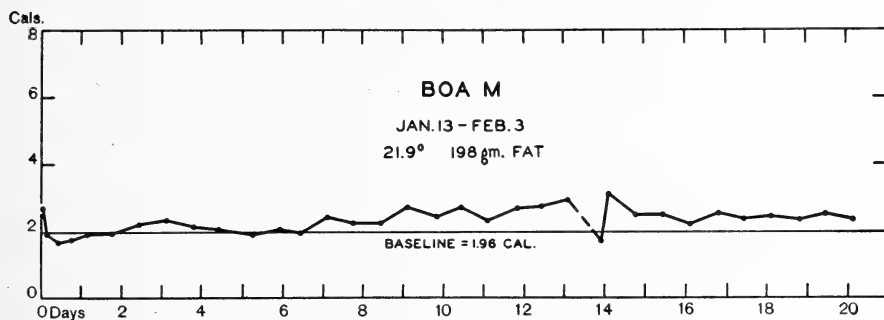


FIG. 82—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO DAYS AFTER FAT INGESTION—Boa M.

Date of digestion experiment, average environmental temperature during experiment, and amount of fat fed to snake are indicated on chart near curve. *Standard* heat production per kilogram of body weight per 24 hours, at same environmental temperature as that of digestion experiment, is shown by "baseline" below curve. That portion of curve shown as broken line represents time when respiration chamber was opened to see if snake was all right.

The metabolism tended to be perceptibly above the initial predigestive level throughout the entire time. No peak that can not be accounted for by activity or disturbance, such as opening the chamber, is to be noticed. Here again there is evidence that with the snake the digestion of fat at a relatively low temperature, 21.9° C. or considerably below the melting point of beef fat, is a long drawn-out process. In this instance the stimulating effect of the fat ingestion on metabolism continued for 21 days. At the end of the experiment on February 3 fatty feces were again found in the chamber. On this date, boa M was returned to the reptile house, and it was reported to have shed its skin, probably on February 6. The results of the experiment are shown graphically in figure 82, which needs no particular comment.

#### COST OF DIGESTION OF FAT WITH SNAKES

Since it was possible to feed these snakes forcibly with fat, the amount of fat and the time of feeding could be controlled. The process of forced feeding results in considerable muscular and probably nervous irritation, to which the metabolism of the snake always reacts. But, as has already

been seen, the general picture is an absence of a pronounced peak in metabolism following the ingestion of fat, such as was usually found in the protein experiments. The metabolism was sustained at a level higher than the predigestive level for many days and in only a few instances had it returned to the baseline when the experiment was terminated. Obviously any attempt to calculate the excess heat production following fat ingestion and particularly to refer the excess heat production to the calories of the intake would be at best crude, for if the baseline has not been reached at the end of the experiment, there is no means of predicting how much longer the metabolism would remain above it and at what elevation. Furthermore, the fat was poorly digested. In four of the seven experiments with fat, fatty feces were found in the respiration chamber after the experiment. The ingestion of 200 or more grams of beef fat by a snake weighing from 4 to 8 kg. represents literally an enormous meal, and it is not surprising that the fat was not better digested. But our object was to give as large an amount of fat as possible, in order to secure a maximum rather than a minimum effect. Although admitting, therefore, that the calculation of the excess heat production in these fat experiments is at best debatable, we have made the computations for each experiment in order to obtain some conception as to what the stimulus to metabolism may be expected to be as a result of the prolonged process of fat digestion. In addition, the calculation has been made of the percentage of the total calories ingested in the form of beef fat (not including the pelt of the rabbit or the guinea-pig) represented by the excess heat production. This percentage has been termed the "cost of digestion" of fat, in the sense as previously employed by Benedict and Carpenter.<sup>1</sup> The results are recorded in table 94.

In the first fat experiment with boa G from May 16 to 30, the metabolism had by no means returned to the predigestive level at the end of the period of observation, but was still very high even at the end of 13 days. In accordance with the method outlined on page 299 in the discussion of the increased heat production following protein ingestion, we have computed that the excess heat production during this experiment was 201 total calories. The boa, which weighed 8.6 kg., had received 227 grams of fat, which have been computed to have an energy content of 2043 calories on the assumption that each gram of fat has an energy value of 9 calories. The excess calories produced, therefore, represented 10 per cent of the caloric value of the intake. There are, however, two factors that vitiate this percentage. One is the fact that the increase in heat production had by no means ceased at the end of 13 days, but that the metabolism was still 65 per cent above the baseline. The other is that the amount of fat actually digested represented considerably less than 2043 calories.

It is conceivable that an experiment in which the baseline was reached might be more helpful in interpreting the stimulus due to food in relation to the intake. Fortunately in the second experiment with boa G, from June 12 to 25, the metabolism returned more nearly to the predigestive level at the end of 13 days. In this experiment a much larger amount of

<sup>1</sup> Benedict, F. G., and T. M. Carpenter, Carnegie Inst. Wash. Pub. No. 261, 1918, p. 335.

fat was given, 340 grams. On the other hand, the excess heat production, 124 calories, was not much more than half that in the first experiment. The computed energy in the fat was 3060 calories. The excess heat production therefore represented but 4 per cent of the energy intake. In this case the evidence was that the stimulus to metabolism had practically, although not completely, ceased at the end of nearly two weeks, in spite of the much larger amount of fat ingested. If the experiment had been continued until the stimulus to metabolism had entirely disappeared, however, the calculated excess in heat production would be greater and thus the percentage relationship between the excess calories produced and the calories of the intake would be increased. On the other hand, the amount of fat actually digested is unknown. The 170 grams of feces passed during the experiment were very fatty. Correction for the undigested fat would

TABLE 94—*Cost of digestion of fat with snakes*

Snake	Date of digestion experiment	Environmental temperature	Weight of food <sup>1</sup> as per cent of snake's weight	Calories in fat	Excess calories produced above baseline	Cost of digestion of fat
		°C.	p. ct.			p. ct.
Boa G	May 16–30	29.4	3	2043	201	10
Boa G	June 12–25	29.6	5	3060	124	4
Boa H	July 6–16	30.1	8	4086	102	2
Boa J	Dec. 5–22	20.9	6	1782	68	4
Boa J	Dec. 30–Jan. 10	31.5	8	2043	79	4
Boa J	Feb. 4–12	31.6	5	1566	27	2
Boa M	Jan. 13–Feb. 3	21.9	6	1782	31	2

<sup>1</sup> Including both fat and rabbit pelt.

reduce the metabolizable fat in the intake and this would result in an increased percentage relationship between the excess in energy output and the energy intake. Consequently the figures given in the last column of table 94 represent in every case minimum percentages that are considerably lower than the actual facts.

With boa H but one fat digestion experiment was made. The amount of fat ingested was large and the environmental temperature high. The heat production instantly increased after the fat had been fed to the snake, and the tendency was for a continually increasing metabolism throughout the 10 days of the experiment, since the results were highest on the last three days. The baseline was therefore by no means reached. Under these conditions and in view of the large intake of fat, it is true that the computed excess in heat production, 102 calories, and the computed cost of digestion of fat, 2 per cent, are minimum figures.

In the protein experiments with boa J, the metabolism returned to the baseline in two out of four instances, and in two of the three fat experiments this also occurred. In the first experiment, from December 5 to 22, the baseline was not reached. In this case 198 grams of fat with a computed energy value of 1782 calories resulted in an increase in heat production of 68 calories, or 4 per cent of the energy intake. The metab-

olism was still 107 per cent above the baseline at the end of 17 days, however. In the next two experiments, from December 30 to January 10 and from February 4 to 12, the metabolism did return to the baseline, but the cost of digestion of the fat was different in these two instances, probably in part because of the difference in the amounts of fat eaten. In the experiment from December 30 to January 10 there were apparently two peaks in the metabolism, and a high level above the baseline was sustained for 9 days. Thereafter the metabolism rapidly returned to the predigestive level. In this experiment the increase in heat production amounted to 4 per cent of the energy intake. Here the only factor of uncertainty is the amount of fat actually digested. In the third experiment, from February 4 to 12, the metabolism again returned to the baseline, and this time rather early, that is, in 7 days, although to be sure the amount of fat ingested, 174 grams, was the smallest in this case. The excess heat production amounted to 27 calories, representing 2 per cent of the computed caloric intake.

With boa M an attempt was made to continue the measurements long enough to be certain that the metabolism had returned to the baseline. In this experiment boa M was fed 198 grams of fat on January 13. The experiment was continued for almost 21 days, but at the end of that time the baseline had not been reached. The increase in heat production amounted to 31 calories and the cost of digestion to 2 per cent.

In none of these calculations shown in table 94 has the specific dynamic action of the rabbit or guinea-pig pelt been taken into consideration. There were probably about 3 grams of nitrogen in the pelt, and undoubtedly in any more subtle analysis of the results the nitrogen in the pelt should not be overlooked. It is not at all impossible that an appreciable percentage of the increase in heat production may be attributed to the pelt alone. An experiment perhaps should have been made in which the pelt alone was eaten. This was not carried out. But in view of the fact that the metabolism did not as a rule return to the predigestive baseline and in view of the uncertainty as to the actual amount of fat digested, it has seemed best not to attempt to correct the calculations of the cost of digestion of fat for the nitrogen in the pelt.

Examination of the data in table 94 shows that, aside from the first value for the cost of digestion of fat with boa G, the other values are 2 and 4 per cent, respectively. The first experiment with boa G, it will be recalled, was one in which the metabolism remained very much above the baseline for the entire period of observation, with no indication of a return to the predigestive level. Since the last two experiments with boa J, however, indicated a return to the baseline, it can perhaps be assumed that the percentages 4 and 2 represent the cost of digestion of fat complicated only by the unknown factor of digestibility. It is highly probable that the fat was at least half digested.<sup>1</sup> In this case the percentages

<sup>1</sup>From analyses of fatty feces collected (see table 24, page 132) one could compute the total amount of undigested fat and refer this to the computed fat in the intake, but the uncertainty as to amount of feces that may logically be ascribed to any particular digestion experiment makes such a procedure not worth while. A rough calculation, based upon figures in hand, has shown digestibilities of fat ranging from but 10 to 45 per cent.

would be increased to 8 and 4, respectively. In all the experiments the cost of digestion of fat was extremely small compared with the cost of digestion of protein. Indeed, from these rough calculations it can be seen that the cost of digestion of fat is not far from that commonly found with humans and dogs and in this particular, therefore, it would seem that the reaction in the metabolism of the cold-blooded snake to the stimulus of fat ingestion is not greatly unlike the reaction noted with warm-blooded animals.

The effect of delayed digestion as the result of a low environmental temperature is interestingly shown in table 94. In the two instances in which the digestion was prolonged by a low temperature, that is, in the first experiment with boa J and in the experiment with boa M, the cost of digestion of fat does not differ from the results found with the other snakes at higher temperatures. With boa J the metabolism was still considerably above the baseline at the end of 17 days, and the unknown continued stimulus would, as has already been pointed out, tend to increase the percentage figure. But with boa M the baseline had been at least approached at the end of 21 days, so that the percentage of 2 would not have been appreciably increased if the experiment had been continued longer. In both cases a second uncertain element is the amount of fat digested. Seemingly, however, there is no material difference whether the fat digestion takes place at 21° or 31°, so far as the general picture of the stimulus to metabolism resulting from the ingestion of fat is concerned.

In studying the effect of the ingestion of food one always has in mind, especially in considering cold-blooded animals, the possibility of a mechanical effect. Any one who has seen a giant python devouring a 20-pound pig and has noted the amount of muscular activity necessary for the ingestion of this enormous meal, the constriction effort, the stretching of the gullet, and the great swelling of the snake's body after the pig has been devoured, must realize that the mechanical action might possibly play a rôle. Although we are by no means in sympathy with the "Verdauungsarbeit" theory of Zuntz as an explanation of the increased heat production incidental to the digestion of food, until this theory is ruled out it must be considered as a possibility, especially with these large serpents that eat such enormous meals. Emphasis again must be laid upon the fact that the individual meal of a snake usually is a gigantic one when compared with the ordinary meal of a human.<sup>1</sup> For example, the total basic 24-hour energy needs of boa H under standard conditions at a temperature of 30° C. may be considered to have been 20 calories just

<sup>1</sup>As an example of the inconceivably large mass of food taken by the snake at one time, see the illustration given by F. Dofflein (*Tierbau u. Tierleben, II: Das Tier als Glied des Naturganzen*, Leipzig and Berlin, 1914, p. 150) of a python skinned and opened to show an adult wild pig that had just previously been swallowed. This illustration has been reproduced by T. Barbour (*Reptiles and Amphibians*, Boston and New York, 1926, fig. 40, p. 40). F. W. FitzSimons (*Pythons and their Ways*, London, 1930, p. 62) gives a photograph of a python after it had swallowed a buck, hind quarters first. The photograph shows that the horns perforated the stomach and skin of the snake. On the same page is a photograph of a South African python after swallowing a half-grown leopard. FitzSimons makes numerous references to the distention of the throat and body of the snake.

prior to the fat digestion experiment carried out with it. The computed calories in the fat ingested (not digested) correspond to 4086, that is, two hundred times the total daily basic requirement. The only instance we know of with humans in which an enormous meal was taken at one time is that reported by Benedict and Carpenter,<sup>1</sup> whose subject, A. H. M., ate a heavy breakfast having a total fuel value of 4378 calories. His basal 24-hour energy requirement was 1704 calories. Thus, in eating this meal the subject obtained somewhat more than twice his total basal daily energy needs. In this case there was a large increase (nearly 40 per cent) in metabolism, indeed so great that part of it may well be ascribed to the mechanical as well as to the chemical processes of digestion.

The habit of these large serpents of eating enormous meals at one time is shown by the record of the feedings of the 32-kg. python. Thus, on June 20, 1916, the python ate a 10-pound pig; on July 18 a 20-pound pig; and on August 1 a 4-pound pig. The energy value of the 20-pound pig may be estimated approximately to be 44,000 calories.<sup>2</sup> According to table 54 (p. 205), the standard heat production of this python at about 30° C. (which is the usual environmental temperature of the snake in its den) was 106 calories per day. Hence at one meal, so to speak, this python ate four hundred times its daily energy needs. It would therefore not be at all surprising if a part, at least, of the increase in heat production following the ingestion of fat in the case of the snakes listed in table 94 was due, on the first day, to the mechanical effect. This possibility, on the one hand, and the possibility, on the other, that the metabolism reacted to a certain extent to the protein of the pelt would tend to compensate perhaps wholly for the unknown factor of the amount of fat undigested. One would therefore probably be not far from right in considering that the average of the figures in the last column of table 94, excepting the first figure for boa G, represents the cost of digestion of fat with snakes. It is clear, however, as pointed out later (see page 326), that further study is needed of the digestive processes of these cold-blooded animals and particularly the intermediary metabolism, and the possible rôle of fatty acids in sustaining the metabolism at a level above the baseline for long periods of time.

The amounts of food eaten by a giant python will obviously depend in large part upon the environmental temperature, that is, upon the metabolic level. This may be sufficiently high to call for a very large food consumption. Dofflein<sup>3</sup> states that in the Trivandrum Museum in Travancore, Southern India, in 1903 a 7-meter python that had shed its skin four times in a year ate in the course of a year 100 hens, a dog, a kangaroo, and four smaller animals. A second snake, 5 meters long, ate in the same time 54 hens, 2 dogs, 2 guinea-pigs, and 5 other small animals. Dr. Ditmars stated to the writer in personal correspondence

<sup>1</sup> Benedict, F. G., and T. M. Carpenter, Carnegie Inst. Wash. Pub. No. 261, 1918, pp. 315-316.

<sup>2</sup> See Armsby, H. P., *The Conservation of Food Energy*, Philadelphia, 1918, p. 23. He considers that one pound of live weight of a medium hog contains about 2186 calories.

<sup>3</sup> Dofflein, F., *loc. cit.*

that at the New York Zoological Park a giant python (7 meters) ate fifty 5-pound roosters in the course of a year. It would seem as if the snake in captivity eats much less than the snake in the wild.

These cold-blooded animals have an extraordinarily low metabolism, which does not approximate that of warm-blooded animals, and yet their optimum temperature, at least that of the animals we studied, is probably only 7° below the body temperature of most warm-blooded animals. The ability of the cold-blooded animal to digest enormous amounts of food at one time and the general inactivity of most of these animals, particularly the snake, make for an economy in nutrition that is unique. Since it is possible, for example, for a python or a boa to eat at one meal two or three hundred times its daily needs, the energy expense of securing for the body this amount of nourishment is extremely small. In the wild, the snake travels a relatively short distance to some water hole or some tract near a water hole where it waits until the prey comes along. The attack is immediate, and for perhaps 20 minutes the activity of the snake is vigorous. At the end of this time the prey has usually not only been killed, but completely swallowed. The snake now has enough food to meet its needs for possibly several months. With no other animals in the world, certainly among the vertebrates, can one expect such economy in the taking of food. In view of this economy in energy expenditure, one can easily understand how it is possible for a large snake to exist for a year or longer without food. At the lower temperatures the metabolism is greatly decreased, and the habit of many snakes (enforced upon them perhaps by climatic conditions) of semi-hibernation or dormancy makes for an extremely small energy consumption. It is not inconceivable, therefore, that a snake might take at one meal enough food to keep it in nutritive equilibrium throughout an entire year, if part of the time is spent in a dormant state.

#### COMPARISON OF EFFECTS UPON METABOLISM OF DIGESTION OF PROTEIN AND OF FAT BY SNAKES

With all the snakes, the influence upon metabolism of the ingestion of protein was rapid and extensive. The peak effect with protein, that is, the maximum percentage increment above the baseline, was much greater than that noted with man, amounting frequently to 300 per cent or over, whereas with humans and dogs the maximum increment in heat production caused by protein ingestion is rarely over 40 per cent. Humans, however, can not eat such an enormous amount of protein at one time as can the snake.

In the two protein digestion experiments with snakes reported by Buytendijk<sup>1</sup> (see page 248 of this report) the metabolism was in neither case even doubled after the ingestion of the food, and there was no indication of a sharp peak in the heat production. The environmental temperature, however, was low (19°) and at the low temperatures, as our data have shown, the reaction to food ingestion is a long drawn-out proc-

<sup>1</sup> Buytendijk, F. J. J., Proc. Section of Sc., Royal Acad. Sci., Amsterdam, 1910, **13**, p. 48; *ibid.*, Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd., 1910, **18**, p. 870.



ess. Evidently the reaction of Buytendijk's boa constrictors to protein was considerably less than that of our serpents, for in all our experiments the stimulus resulting from the ingestion of protein was striking, even at 16° or 17° C. Most of our protein experiments, however, were made at temperatures higher than those of Buytendijk, which may explain the difference in the findings.

Although this report is concerned chiefly with the metabolism of large cold-blooded animals, it is interesting to note that Bialaszewicz<sup>1</sup> has reported digestion experiments with the leech, in which the ingestion of one gram of food (more than 160 times the daily basal needs of an animal weighing about one gram) increased the metabolism about 120 per cent above that during fasting. This may be compared directly with the maximum increase in heat production above the baseline of 300 per cent or over found by us with large snakes after protein ingestion. Bodine<sup>2</sup> has recorded certain observations on digestibility with starved grasshoppers, in which he measured the carbon-dioxide output following feeding. The temperature was not far from 21° C. The response to taking food was immediate, the carbon-dioxide production being approximately doubled 3 hours after feeding, with a tendency for a still further rise continuing for some time. In no case, however, was the percentage increment as high as noted in our snakes. The experiments of Elsas<sup>3</sup> with frogs showed noticeable increases in metabolism after protein and carbohydrate feeding, and but small increases following fat feeding.

Following the ingestion of fat the metabolism of our snakes was increased, but there was no sudden, sharp rise. The increase was at a lower level than that after protein, only about 50 or 100 per cent above the baseline, but was sustained for a long time with, in most instances, no indication of a return to the predigestive level even after many days. It is clear that in connection with the problem of the effect of fat digestion with snakes the intermediary metabolism should be studied, particularly that phase involving the possible effect of fatty acids and acidosis. It would appear as if the chemistry of the digestive processes of these cold-blooded animals was well worthy of study, since almost nothing is known about the intermediary metabolism. In his study on digestive enzymes in poikilothermal vertebrates, Kenyon<sup>4</sup> has studied, among the reptiles and amphibians that we are especially interested in, the Bull Snake or *Pituophis sayi* (Schlegel) and the turtle. Bearing upon the question of the chemistry of digestion, Kenyon points out that the greatest acidity he observed was in a bull snake, the stomach of which contained the remains of two mice still largely intact, which had been devoured two days before killing. Here the hydrogen-ion concentration was almost pH 3, but no acidity could be demonstrated in the stomach of a

<sup>1</sup> Bialaszewicz, K., *Études comparées sur le métabolisme chimique et énergétique. I. L'inanition et la nutrition chez les Hirudinées*, Travaux Soc. d. Sci. d. Varsovie, III. Classe d. sc. math. et naturelles, No. 32, 1919. (In Polish. See French résumé at end, p. 113.)

<sup>2</sup> Bodine, J. H., *Journ. Exper. Zool.*, **32**, p. 137.

<sup>3</sup> Elsas, B., *Der Einfluss der Nahrungszufuhr auf den Gaswechsel des Kaltblüters*, Dissertation, Marburg, 1913.

<sup>4</sup> Kenyon, W. A., *Bull. Bureau Fisheries, Document No. 977, 1925*, **41**, p. 181.

fasting bull snake. In the stomachs of garter snakes that had swallowed frogs one to three hours before being opened, a similar region of acidity was observed around the frogs.

With regard to the mechanical effect, it is true that the act of ingesting a large mass of food representing, as in many of our experiments, on the average from 7 to 8 per cent of the body weight of the snake (often a much larger percentage when animals as large as a pig are eaten) must have some effect. Peristalsis as such could hardly be of any great effect, and in these fat experiments there was undoubtedly a persistent stimulus to metabolism which asserted itself even at an environmental temperature which is low for snakes.

TABLE 95—*Increase in metabolism of snakes above standard needs after ingestion of protein and fat*

Snake	Date of digestion experiment	Body weight	Excess calories due to—	
			Protein	Fat
		<i>kg.</i>		
Python.....	3 expts. at 22°..	6.31	<sup>1</sup> 90	....
Boa J.....	Oct. 26-31....	4.18	<sup>2</sup> 52	....
Boa J.....	Nov. 6-12....	4.32	<sup>2</sup> 66	....
Gopher snake A.	Sept. 11-18....	3.01	<sup>3</sup> 37	....
Boa G.....	May 16-30....	8.62	....	<sup>1</sup> 201
Boa G.....	June 12-25....	8.38	....	<sup>3</sup> 124
Boa H.....	July 6-16....	6.97	....	<sup>1</sup> 102
Boa J.....	Dec. 5-22....	4.32	....	<sup>1</sup> 68
Boa J.....	Dec. 30-Jan.10	3.91	....	<sup>2</sup> 79
Boa J.....	Feb. 4-12....	4.04	....	<sup>2</sup> 27
Boa M.....	Jan. 13-Feb.3.	4.05	....	<sup>3</sup> 31

<sup>1</sup>Metabolism had not returned to the predigestive baseline.

<sup>2</sup>Metabolism had returned to the predigestive baseline.

<sup>3</sup>Metabolism had nearly returned to the predigestive baseline.

The effect of the ingestion of food upon the heat production of the snake may be considered from another standpoint, that is, the comparison of the total excess calories produced due to the ingestion of protein and fat. Is it possible that the sustained, low increase in metabolism with fat ingestion may result in a total excess heat production equal to the total excess heat production that follows protein ingestion, even although in the latter case the maximum percentage increment above the baseline is greater and the duration of the effect is shorter? The calculation of the total excess calories produced is most accurately made in those cases where the snake's metabolism returned to the predigestive level after a meal. This happened in two experiments, both with protein and with fat. In the other experiments the metabolism did not return to the baseline and in these cases the estimation of the excess calories represents a minimum value. In table 95 are recorded the excess calories produced above the standard requirements of the snake for all the fat experiments, whether the baseline had been reached after the food

was given or not, and for those protein experiments in which the baseline was either definitely or approximately reached. In this table no attempt has been made to compare the excess calories produced with the calories ingested, for, as has already been pointed out in the case of fat particularly, a considerable proportion of the meal passed through the body undigested. In the fat experiments also, no correction has been made for the effect of the nitrogen in the pelt, but probably this pelt could account for a rise of but relatively short duration.

Comparison of the effect of protein and the effect of fat *with the same snake* can be made only in the case of boa J. Examination of the data in table 95 shows, surprisingly, that there is practically no difference in the resulting excess heat production, whether a lump of only partly digestible fat is ingested or whether a completely digestible, highly nitrogenous rabbit is devoured. This comparison is without reference to the peak effect in metabolism or the total amount of calories in the intake. The fact is that the introduction of beef fat into several snakes resulted in an excess heat production above the baseline approximating that resulting from the ingestion of relatively large amounts of animal flesh. The theory that this increase in heat production due to fat is wholly explained by the mechanical action seems hardly tenable, as has already been pointed out in our earlier discussion. On the other hand, the theory of a chemical stimulus seems plausible, especially when one considers the possibility for the presence of acids, fatty acids particularly, in such a digestive procedure. These considerations strongly urge the importance of studies of intermediary metabolism during the process of digestion particularly of fat, with large cold-blooded animals.

## GASEOUS METABOLISM AND ENERGY TRANSFORMATIONS OF LARGE ALLIGATORS

Although in the literature<sup>1</sup> a few respiration experiments have been reported with alligators or crocodiles of small size, no large crocodiles or alligators have been studied by other investigators, so far as their respiratory exchange is concerned.<sup>2</sup> On March 21, 1916, an alligator (*Alligator mississippiensis*—Daudin) weighing 53.4 kg., with a length over-all of 224 cm., was placed in the large respiration chamber with recessed cover, having an air volume of 339 liters (fig. 3, p. 21). The carbon-dioxide production was measured without interruption for seven continuous periods, at an environmental temperature remaining essentially at 22° throughout this time. At the end of seven periods there was an interval of about three-quarters of an hour, and then three more con-

<sup>1</sup>Krehl, L., and F. Soetbeer, Arch. f. d. ges. Physiol., 1899, **77**, p. 611. See, also, Buytendijk, F. J. J., Proc. Section of Sc., Royal Acad. Sci., Amsterdam, 1910, **13**, p. 48; *ibid.*, Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd., 1910, **18**, p. 870.

<sup>2</sup>Among other animals, Isserlin (Arch. f. d. ges. Physiol., 1902, **90**, p. 472) reports temperature observations on a 14.75-kg. alligator, 1.75 meters long. The animals were studied in dry air, saturated air, and water. Isserlin found no difference between the temperatures of the animals and that of the medium surrounding them, when they were in water. In dry air the animals were colder, and in moist air they had the same or a somewhat higher temperature than that of the air.

secutive periods were carried out on March 22-23, although unfortunately at a somewhat lower temperature, 19.5° C. The results are given in table 96. The usual high metabolism following the placing of a cold-blooded animal inside the chamber, particularly following struggle and activity, was found at the beginning of the measurements. Indeed, the effect of the activity did not disappear for practically three hours, although there was a constantly decreasing metabolism from the first to the fourth period. In the fifth, sixth and seventh periods the metabolism became sufficiently uniform to justify considering the results as approximating the standard metabolism. The values for the carbon-dioxide pro-

TABLE 96—*Metabolism of a 53-kg. alligator*

Date	Period		CO <sub>2</sub> per kg. per 24 hours		Heat produced per 24 hours		Environ- mental tempera- ture
	No.	Length	Period values	Average	Per kg.	Per sq. m.	
1916		<i>mins.</i>	<i>gm.</i>	<i>gm.</i>	<i>cal.</i>	<i>cal.</i>	°C.
Mar. 21	1	60	3.604				21.7
Mar. 21	2	60	1.672				21.7
Mar. 21	3	60	.661				22.0
Mar. 21	4	60	.360				22.9
Mar. 21	5	90	*.337				
Mar. 21	6	285	*.255	10.299	11.00	129.9	22.1
Mar. 21-22	7	665	*.313				
Mar. 22-23	1	260	*.364	1.256	1.85	125.4	19.5
Mar. 22-23	2	444	*.211				
Mar. 22-23	3	720	*.247				

\* Starred data only represent the standard metabolism.

<sup>1</sup> In obtaining this average value, starred period values for carbon dioxide were weighted according to length of period.

duction measured during these periods have, therefore, been averaged, being weighted according to the length of each period, and the average has been found to be 0.299 gram of carbon dioxide per kilogram of body weight per 24 hours. The alligator was not disturbed between the first and the second series of observations. The weighted average carbon-dioxide production during the last three periods, on March 22-23, which lasted practically 24 hours, was 0.256 gram or 14 per cent less than the average obtained in the experiment of the day before. There was, however, a decrease in temperature of 2.6° C.

There was some activity in the various periods. Indeed, the alligator was by no means as quiet as the average snake. One difficulty with the alligators and the lizards was the inability to eliminate completely extraneous activity. In the periods starred in table 96 the activity was at a minimum, however, and the measurements recorded for these starred periods represent fairly close approximations of the standard metabolism under the prevailing temperature. The food eaten by this alligator before the experiment is not known. The animal was taken from a large

pool and probably had not been fed for at least three days. Certainly in the second experiment, on March 22-23, the alligator had been fasting longer than in the first experiment, but the metabolism was much the same as in the first experiment, if one makes due allowance for the fall in temperature.

A second alligator, weighing 4.4 kg., was also studied during five consecutive periods covering two full days, in the hope of securing sufficiently quiet periods to designate the measured metabolism as standard. The environmental temperature averaged 18.1° C. This alligator moved continually, and as a result the carbon-dioxide production per kilogram of body weight per 24 hours was 1.329 grams and the heat production on the same basis 4.42 calories. These results are cited only to show that the metabolism of a small, but active alligator may be four or five times that of a larger alligator at rest. How much of this difference in metabolism is to be ascribed to activity and how much to size can be only the basis of speculation. It is believed, however, that a large part of it can be ascribed to activity, for in one of the five periods with the 4-kg. alligator the carbon-dioxide production was as low as 0.835 gram per kilogram of body weight per 24 hours, and even in this period there was some activity. For the 53-kg. alligator, however, the standard metabolism was definitely established to be on the average 1.00 calorie per kilogram of body weight per 24 hours at 22.1° and 0.85 calorie at 19.5° C. It was impracticable to continue the experiments with alligators, although it is clear that further observations with this animal and particularly with its near zoological associate, the crocodile, should be made. Observations on the alligator would be especially important in contributing to the interesting point raised by Krogh<sup>1</sup> that the metabolism of tropical cold-blooded animals may vary considerably from that of cold-blooded animals normally living in a colder environment, even if both are measured at the same environmental temperature. This subject has likewise been discussed by Buytendijk.<sup>2</sup>

With the 53-kg. alligator an extensive series of measurements of girths and lengths was made with the idea of attempting to calculate the surface area from them, but the irregular shape of the alligator makes the value of such a calculation doubtful. We have, therefore, not used these measurements but instead have calculated the body surface from the two-thirds power of the body weight, employing Inaba's constant of 12.6 for the lizard, as suggested by Rubner.<sup>3</sup> Theoretically, we should have used the constant actually employed for our own series of lizards, namely, Martin's constant<sup>4</sup> of 10. The body surface of the 53-kg. alligator, based upon the constant 12.6, has been computed to be 1.79 square meters and that of the 4-kg. alligator, 0.34 square meter. The average standard heat production per square meter of body surface per 24 hours of the 53-kg. alligator would thus be 29.9 calories at 22.1° and

<sup>1</sup> Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, p. 101.

<sup>2</sup> Buytendijk, F. J. J., *Proc. Section of Sci., Royal Acad. Sci., Amsterdam*, 1910, **13**, p. 48; *ibid.*, *Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd.*, 1910, **18**, p. 870.

<sup>3</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 273.

<sup>4</sup> Martin, C. J., *Philos. Trans., B.*, 1903, **195**, p. 1.

25.4 calories at 19.5°. The heat production of the 4-kg. alligator was 57.2 calories per square meter of body surface at 18.1° C., but this value may not be considered to represent the standard metabolism because of the animal's great activity. These results will be referred to subsequently, when the comparison of the metabolism of all the different species of cold-blooded animals is made (see p. 428).

Among the cold-blooded animals studied by Buytendijk<sup>1</sup> was an alligator weighing 530 grams. The heat production of this alligator at 18° to 19° C. has been calculated to be 6.74 calories per kilogram of body weight per 24 hours. Our 53-kg. alligator, which weighed one hundred times that of Buytendijk, had a heat production per unit of weight of only 0.85 calorie at 19.5° C. On the surface-area basis our 53-kg. alligator produced 25 calories, as compared with the calculated heat production of Buytendijk's alligator of 43 calories per square meter of body surface per 24 hours. Thus the comparison is closer on the surface-area basis.

## GASEOUS METABOLISM AND ENERGY TRANSFORMATIONS OF LARGE LIZARDS

The lizards are an excellent example of terrestrial cold-blooded animals.<sup>2</sup> The supply at the New York Zoological Park was large, and hence it was possible to secure a number of these animals for study. The experimental specimens varied in weight from only 0.91 to 1.30 kg. The measurements on these lizards, of which there were seven specimens, thus give an excellent means of comparing the metabolism of different animals of the same species (South American Iguanas, *Iguana tuberculata*). The observations were all made between May 29 and July 19 at environmental temperatures between 25.6° and 31° C., that is, in moderately warm weather. The results of the carbon-dioxide measurements are recorded in table 97, together with the derived calculations of the 24-hour heat production per kilogram of body weight and per square meter of body surface. The heat values have been obtained by assuming a respiratory quotient of 0.72.

An uncertain factor entering into these results is the question of how long the lizards had been without food. The seven specimens were taken from the cage in which the lizards were kept, and had in no case eaten just prior to the experiments. In all probability they had been without food for several hours. With lizard II alone is the exact time after food known. This lizard was last fed on May 31, prior to the series of observations from June 5 to 11.

<sup>1</sup> Buytendijk, *loc. cit.*

<sup>2</sup> As Barbour (*Reptiles and Amphibians*, New York, 1926, p. 5) has so aptly pointed out, "It is customary to call snakes 'primitive' and 'degenerate' because they seem relatively simple in appearance. In fact, however, they represent extreme modification, whereas the apparently more highly organized and really ancestral lizards seem to the average observer a 'higher' type of development. Lizards are simply to be considered the more generalized, more typical or less modified group of the vertebrates from which the snakes have sprung."

The activity recording device inside the respiration chamber made possible a reasonable certainty regarding the degree of activity during the

TABLE 97—*Metabolism of lizards*<sup>1</sup>—Fasting

Lizard and date	Length of expt.	CO <sub>2</sub> per kg. per 24 hours	Heat produced per 24 hours		Environmental temperature
			Per kg.	Per sq.m.	
1916	hrs.	gm.	cal.	cal.	°C.
Lizard I:					
May 29-30.....	19	*1.337	4.46	48.4	29.1
May 31-June 1...	22	*1.017	3.39	36.8	26.8
June 1-2.....	24	1.417	.....	.....	28.8
June 2-3.....	23	2.121	.....	.....	28.7
June 3-4.....	15	*1.298	4.33	47.0	30.1
Lizard II:					
June 5-6.....	20	*1.245	4.15	43.0	27.0
June 6-7.....	25	*1.274	4.25	44.0	25.6
June 7-8.....	19	*1.601	5.34	55.3	27.7
June 8-9.....	17	*1.493	4.98	51.6	29.5
June 9-10.....	22	*1.078	3.59	37.2	26.0
June 10-11.....	18	*1.084	3.61	37.4	26.0
Lizard III:					
June 19-20.....	17	2.679	.....	.....	26.6
June 20-21.....	19	2.062	.....	.....	26.5
June 21-22.....	20	*1.438	4.79	50.3	26.5
June 22-23.....	19	*1.356	4.52	47.5	26.5
June 23-24.....	20	*1.428	4.76	50.0	26.1
June 24-25.....	20	*1.900	6.33	66.5	26.4
Lizard IV:					
June 26-27.....	15	1.804	.....	.....	26.7
June 27-28.....	22	1.489	.....	.....	26.7
June 28.....	9	*1.127	3.76	41.0	26.2
June 29-30.....	20	*1.627	5.42	59.2	30.4
June 30-July 1...	20	*1.470	4.90	53.5	30.9
July 1-2.....	21	*1.115	3.72	40.6	26.8
Lizard V:					
July 3-4.....	19	*1.271	4.24	43.9	27.5
July 5-6.....	18	*1.157	3.86	40.0	27.3
July 6-7.....	20	*1.589	5.30	54.9	29.5
July 7-8.....	21	*1.700	5.67	58.7	29.7
July 8-9.....	21	*2.619	8.73	90.4	31.3
Lizard VI:					
July 10-11.....	20	*1.700	5.67	57.1	27.1
July 11-12.....	20	*2.130	7.10	71.5	31.0
July 12-13.....	21	*2.315	7.72	77.7	31.0
July 14-15.....	20	*2.193	7.31	73.6	30.5
July 15-16.....	17	*1.887	6.29	63.3	30.7
Lizard VII:					
July 17-18.....	12	*2.065	6.88	66.7	30.5
July 18-19.....	20	*1.935	6.45	62.5	30.6

\* Starred values only represent standard metabolism.

<sup>1</sup> Lizard I weighed 1.28 kg.; lizard II, 1.11 kg.; lizard III, 1.16 kg.; lizard IV, 1.30 kg.; lizard V, 1.11 kg.; lizard VI, 1.02 kg.; lizard VII, 0.91 kg.

experiments. It is believed that the periods starred in table 97 represent periods of relative, if not absolute, quiet. Certainly the kymograph records did not indicate sufficient activity to justify discarding them.

These starred values alone may be considered as representing the standard metabolism.

Because of the slight changes in environmental temperature from day to day, the data for the different days may not be directly compared without considering at the same time the temperature of the environment. The starred values for any individual lizard show a general tendency to be reasonably uniform, if due allowance is made for temperature changes.

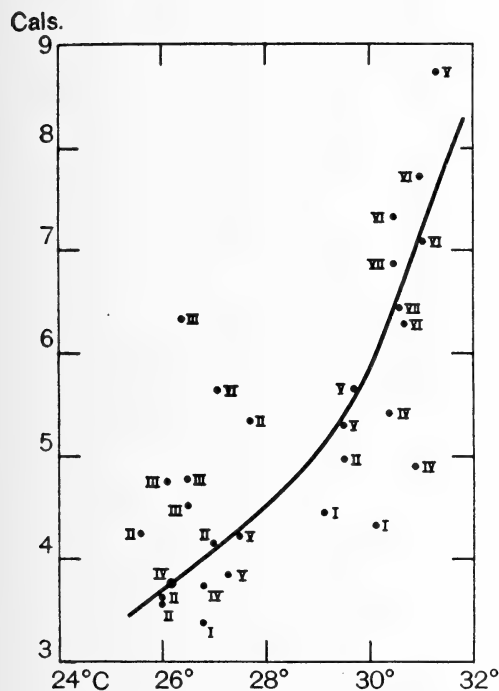


FIG. 83—STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—LIZARDS.

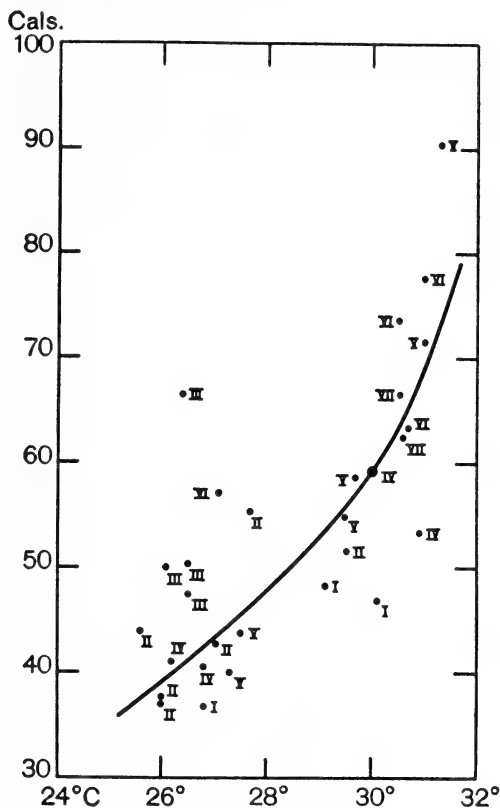


FIG. 84—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—LIZARDS.

Individuality of lizards is indicated by Roman numerals against plotted points.

One striking exception is the series of observations with lizard III. From June 19 to 25 the temperature hardly changed, and yet after the first two periods in which activity entered, the metabolism was relatively uniform until June 24-25. On this day, during a period lasting 20 hours, the carbon-dioxide production increased greatly, and there is no adequate explanation for the increase. There is no alternative, therefore, except to include this value among the starred data.

The best procedure for comparing the metabolism of the different lizards is to plot the starred heat values with reference to environmental



temperature. The data computed per kilogram of body weight are shown in figure 83. The plotted points are widely distributed, and the point for lizard III at  $26.4^{\circ}$ , just discussed in the above paragraph, lies much higher than the other observations. It is difficult to lay on a curve that would be representative of these various points, and yet this has been done, primarily for purposes of approximate comparison of these lizards with other cold-blooded animals and not to present a curve from which the metabolism of any individual lizard could be predicted, if the body weight and the environmental temperature were known.

*Body surface constant for lizards*—The differences in the weights of these seven lizards are relatively so small that one would hardly expect any change in the picture when the metabolism is computed per square meter of body surface. This calculation introduces the question of the constant to be used in estimating the surface area. Rubner,<sup>1</sup> in reporting the results obtained by Krehl and Soetbeer<sup>2</sup> on the lizard, has made use of Inaba's constant of 12.6.<sup>3</sup> For purposes of comparison of animals of the same species, where the body weights are almost uniform, the precise value of the constant is not of great significance. But for the comparison of animals of different species the constant assumes greater significance. Martin<sup>4</sup> reports a constant of 10 for lizards, obtained by direct measurement of the skin after removal from the body. Inaba's constant of 12.6 was determined upon lizards ranging from 4 to 26 grams in weight. The measurements made by Martin were on lizards with weights more nearly that of our own animals, that is, on the average 374 grams. In the computation of the body surfaces of our seven lizards we have consequently used Martin's constant of 10.<sup>5</sup> If a K of 12.6 had been used by us, the results presented in table 97 and figure 83 for the heat production per square meter of body surface would obviously have been 25 per cent lower. Unfortunately differences of 25 per cent in the value of K are only too frequently found in the literature. It is difficult to conceive that there could be an actual difference of 25 per cent in the constant for lizards with such small differences in size as those reported by Inaba and Martin. In Rubner's observations on the skin area of dogs weighing from 225 to 3600 grams, his constant varies from 9.4 to 11.02, that is, the smaller the animal the smaller was the constant. On this basis, if Inaba's constant of 12.6 for the small lizard should be accepted, Martin's actually measured constant of 10 for somewhat larger lizards would seem inconsistent. If the surface area is to be considered as an important factor in relation to the environment, it is obvious that the fish presents the ideal condition. Immersed in water, with a configuration that does not alter appreciably with increasing size or age, the fish should have a remarkably uniform body-surface constant.

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 273.

<sup>2</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 616.

<sup>3</sup> Inaba, R., *Arch. f. Physiol.*, 1911, p. 7.

<sup>4</sup> Martin, C. J., *Philos. Trans., B*, 1903, **195**, p. 1.

<sup>5</sup> The average constant of 11.6 found by Fry for eight lizards (but using a body-weight exponent of 0.68) can hardly play a rôle in our work, since his animals ranged in weight from only 3 to 13 grams. (See Fry, H. K., *Quart. Journ. Exper. Physiol.*, 1913, **7**, p. 191.)

Buytendijk,<sup>1</sup> however, who measured the surface area of small fish, maintains that the constant may vary from 8 with the small *Scyllium* weighing about 9.9 grams to 7 with large fish weighing 108 grams. Although the fish measured by E. Voit<sup>2</sup> varied in weight from only 120 to 251 grams, a slightly smaller value for K was found with the smaller fish. This use of the smaller constant with the larger animal is in line with the finding of Martin of a constant of 10 for a 374-gram lizard as compared with Inaba's constant of 12.6 for a 25-gram lizard.<sup>3</sup>

The values for the heat production per square meter of body surface of our lizards are plotted in figure 84. Rough inspection of this chart shows, as is to be expected, that the general scatter of points is much the same as that noted in the chart for the metabolism per kilogram of body weight. Here again the difficulty of laying on a curve is apparent, but such a curve has been attempted and will be used in subsequent comparisons. Examination of the individual points on this chart indicates that the heat production of the same animal is by no means uniform at the same temperature. Thus, with lizard III at 26.5° there is a low value of 47.5 calories per square meter of body surface and a high value of 66.5 calories. Hence the general trend of the heat production alone is of significance. This shows the usual increase in metabolism with the rising temperature.

Lizard VII was the smallest and lizard I next to the largest of the seven specimens. All the values for lizard I lie distinctly below the average curve representing the trend of the heat production per kilogram of body weight with increasing temperatures, but the two values for lizard VII lie close to the line, although they were obtained at a higher temperature. This suggests that the metabolism may be slightly lower with the larger lizard than with the smaller lizard, a common experience in the comparison of large and small warm-blooded animals on the basis of the heat production per kilogram of body weight. Again, in the chart showing the heat production per square meter of body surface referred to temperature, it is possibly of significance that the two values for lizard I at 29° and 30° lie materially below the curve, whereas the two values for lizard VII at 30.5 lie close to the curve. In other words, the smaller animal appears to have a metabolism slightly higher than that of the larger animal. The differences in body weight are really not sufficient, however, to justify any general conclusion.

The observations by other investigators on the gaseous metabolism of the lizard are confined to the studies of Regnault and Reiset, Pott, Krehl and Soetbeer, Martin, Buytendijk, and Leichtentritt. The observations of Regnault and Reiset<sup>4</sup> are not, for the most part, directly comparable with our data, because obtained at lower temperatures and complicated by the effects of winter sleep and in one instance by the ingestion of food. Buy-

<sup>1</sup> Buytendijk, F. J. J., Proc. Section of Sci., Roy. Acad. Sci., Amsterdam, 1909, **12**, p. 48; *ibid.*, Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd., 1909, **17**, p. 886.

<sup>2</sup> Voit, E., Zeitschr. f. Biol., 1930, **90**, p. 251.

<sup>3</sup> For further consideration of the possibility of differences in the value of the constant with differences in the size of the animal see the discussion of the calculation of the surface area of snakes on pages 144 to 148 and table 28 on page 146 of this report.

<sup>4</sup> Regnault, V., and J. Reiset, Annales de Chim. et de Phys., 1849, 3d ser., **26**, p. 299.

tendijk<sup>1</sup> states that his lizard was very active. Hence his results likewise are not directly comparable. Pott<sup>2</sup> carried out three experiments at temperatures between 17° and 20° on a lizard weighing 0.8 gram. His values for carbon-dioxide production, and hence any computations therefrom of the heat production, either per kilogram of body weight or per square meter of body surface, are extraordinarily high, in large part accounted for by digestion and activity. The lizards of Leichtentritt<sup>3</sup> weighed about 20 grams each and were measured at environmental temperatures ranging from 13° to 33°. Leichtentritt computes that at 33° the heat production

TABLE 98—Heat production of lizards studied by Krehl and Soetbeer and by Martin

Investigator	Body weight	Heat produced per 24 hours		Temperature
		Per kg.	Per sq. m.	
Krehl and Soetbeer <sup>1</sup> . . .	<i>gm.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
	110	19.2	73.0	<sup>2</sup> 25.3
	1250	6.2	53.0	25.3
	110	36.0	136.9	37.0
Martin <sup>3</sup> . . . . .	1250	9.6	82.1	37.0
	374	1.1	7.6	<sup>4</sup> 5.5
		3.4	24.4	9.2
		4.2	30.3	15.2
		4.4	31.6	20.4
		5.1	36.8	24.5
		6.2	44.4	29.3
		7.7	56.0	34.8
		23.3	168.4	38.5

<sup>1</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 611.

<sup>2</sup> Environmental temperatures in this series.

<sup>3</sup> Martin, C. J., *Philos. Trans., B*, 1903, **195**, p. 1.

<sup>4</sup> Rectal temperatures in this series.

per 100 grams per day varied from 4.4 to 6.5 calories. At 13.4°, 25.6°, and 31.6° the heat production on this basis was constant at 2.1 calories, but at 16.9° it was 0.07 calorie.

The measurements made by Krehl and Soetbeer<sup>4</sup> on a 110-gram lizard and a Uromastix weighing 1250 grams were not complicated by the effect of food, since they definitely state that their animals were fasting. The lizards of Martin,<sup>5</sup> which weighed on the average 374 grams each, had been without food for a day before each experiment. The results obtained by Krehl and Soetbeer and by Martin have been summarized in table 98. In the former case the body-surface constant was assumed to be 12.6. Martin actually measured the surface area of some of his lizards and found

<sup>1</sup> Buytendijk, F. J. J., *Proc. Section of Sci., Roy. Acad. Sci., Amsterdam*, 1910, **13**, p. 48; *ibid.*, *Kon. Akad. v. Wetensch., Wis-en Natuurk, Afd.*, 1910, **18**, p. 870.

<sup>2</sup> Pott, R., *Landw. Versuchsstat.*, 1875, **18**, p. 81. Weight of lizard given as 0.8 gram (!!).

<sup>3</sup> Leichtentritt, B., *Zeitschr. f. Biol.*, **69**, p. 545.

<sup>4</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 611.

<sup>5</sup> Martin, C. J., *Philos. Trans., B*, 1903, **195**, p. 1.

the constant to be 10. The heat production of Martin's lizards has been computed from the carbon-dioxide production on the assumption that the respiratory quotient was 0.72. The values for the lizards of Krehl and Soetbeer represent direct calorimetric measurements. Further comparisons of the observations of Krehl and Soetbeer and of Martin with our data and with the data of other investigators on different types of cold-blooded animals will be made subsequently (pages 453 to 462). Here it need only be pointed out that the observations of Krehl and Soetbeer at 25° are much higher than Martin's values or our values found with lizards. (See table 97, p. 332, and figs. 83 and 94, p. 333.) Martin's measurements, on the other hand, are much more in accord with our own results. Thus, our curve for the standard heat production of lizards per kilogram of body weight (fig. 83) indicates that the metabolism at 25° and 30° would be 3.4 and 5.9 calories, respectively, as compared with the calculated values for Martin's lizards of 5.1 and 6.2 calories at these same temperatures. On the body-surface basis (fig. 84) our curve indicates a heat production at 25° and 30° of 36 and 59 calories as compared with 37 and 44 calories with Martin's lizards. In general, therefore, taking into consideration the size of the animals, one can state that our research confirms in a satisfactory manner the careful study of Martin. At 37° the results of Krehl and Soetbeer, which average 110 calories per square meter of body surface, agree reasonably well with the calculated heat values for Martin's lizards at 34.8° and 38.5° C., temperatures beyond the range in which we studied our lizards.

Although we made no observations on the respiration rate of lizards, attention should be given to the study of Langlois<sup>1</sup> on thermic regulation in cold-blooded animals, particularly the lizard. The observations of Langlois, however, were made at very high temperatures, 38° to 44°, since he was interested in the rôle played by polypnœa in the heat loss of these animals.

## PHYSIOLOGY OF LARGE TORTOISES

### PLAN OF RESEARCH

One of the main objects of this research, as already stated, was to study the largest possible cold-blooded animals. In the matter of mere weight alone, no cold-blooded land animal at the present day equals the gigantic tortoises such as those of the Galapagos Archipelago.<sup>2</sup> We were privileged to study the respiratory metabolism of three of these huge tortoises<sup>3</sup> at the New York Zoological Park. In addition, a number of metabolism experiments with smaller gopher tortoises were subsequently made. (See page 8 regarding the species used.) Between 1915 and 1917 seven tortoises were studied, of which three weighed 69, 80 and 132 kg., respectively, and the other four weighed approximately 5 kg. each. For convenience in referring to them, these animals have been assigned letters of the alphabet from A to G, and the experiments made with them will be spoken of as the "series of 1915-1917." With the three largest tortoises (E, F and G) the influence of extremes in environmental temperature obviously could not be studied, for

<sup>1</sup> Langlois, J. P., Journ. de Phys. et de Path. gén., 1902, 4, p. 249.

<sup>2</sup> There are records of crocodiles larger than these tortoises.

<sup>3</sup> Specimens of *Testudo vicina* and *T. nigrita*.

their rarity and cost made any possible jeopardizing of their health out of the question. These three were therefore measured at temperatures ranging only from 19.6° to 24.4° C. With the 5-kg. animals the environmental temperature in the New York series was as low as 18.0° and as high as 31.9° C. The 5-kg. tortoises were studied in the 27-liter chamber, commonly used for snakes (fig. 2, p. 20). The larger ones were studied in the 908-liter chamber built especially for them (figs. 3, 4 and 5, p. 21, 22 and 23).

In a preliminary comparison of the results of the 1915-1917 tortoise series with the results obtained on snakes, lizards and alligators, a wholly unexpected divergence in the metabolism of the tortoise was found. It was therefore decided to make some supplementary experiments on tortoises at the Nutrition Laboratory in the fall of 1930, to confirm the earlier findings and to fill in some of the gaps in the earlier material. Since many of the observations in the 1915-1917 series were made with 5-kg. animals and since the larger tortoises are expensive and difficult to transport, the 1930 series was confined to two tortoises (Y and Z) weighing approximately 5 kg. each. These were South American Gopher Tortoises (*Testudo denticulata*), obtained through the kindness of Dr. R. L. Ditmars from the New York Zoological Park, and were subjected to various types of measurement at the Nutrition Laboratory during September and October 1930. The 1930 experiments were conducted by the same technician as in the earlier series, Mr. E. L. Fox, but a somewhat different technique was employed that enabled accurate determinations of the respiratory quotient (figs. 8, 9 and 10, pp. 28, 32 and 33).

In the 1915-1917 series the carbon-dioxide production only was studied. Because of the small amount of carbon dioxide produced by these cold-blooded animals, the difficulty of exact temperature control with the 908-liter respiration chamber, and the great rôle played by the temperature of the air inside the chamber in the calculation of the oxygen residual in the chamber, it was practically impossible to measure satisfactorily the oxygen consumption of these large tortoises. Such measurements were attempted, but the irregularity in the results was so great that we do not feel justified in reporting them. Hence at the time of these observations it was not clear whether the respiratory quotient of the fasting tortoise would tend to approximate that for fat or more nearly that for carbohydrate. Tortoises are vegetarians and hence would be expected to have a high respiratory quotient when fed. They can exist a great length of time without food, however, and during such time undoubtedly subsist upon body fat, of which they have a liberal supply. The best index as to the probable state of nutrition of these animals is their excreta. When there are considerable amounts of feces, as was noted on occasions, it is fair to assume that they have been feeding recently upon carbohydrate material, with a liberal supply of chopped hay. But the assumption of a respiratory quotient for these experiments made in 1915-1917 would be at best only a rough conjecture. One of the main objects of the 1930 series was therefore to establish definitely the respiratory quotient of the fasting tortoise, so that the calculations of the heat production of the tortoises in the earlier series might be more accurately controlled.

In analyzing the metabolism data for the earlier series, especially for the 5-kg. tortoises, it was found that two animals showed a standard metabolism unquestionably at a much higher level than that of two others, even at the same environmental temperature. Another object of the 1930 series was therefore to determine what the standard metabolism would be of two other 5-kg. tortoises when studied at different environmental temperatures. Inasmuch as tortoises feed well in captivity, it was possible also to note the reaction of their metabolism to the ingestion of moderately large amounts of carbohydrate, with reference both to the respiratory quotient and to the specific dynamic action of the food ingested. Most of the 1930 experiments were made at or near 25° to 30° C., but in a few instances the temperature was as low as 14° and 17° and in one instance as high as 36° C.

The prime object of the investigation with tortoises was to study their respiratory metabolism. Since it is important to correlate the respiratory metabolism with various physiological functions and anatomical factors, numerous observations were made in 1930 bearing upon the general physiology and anatomy of the tortoise. Many of these were admittedly only of a preliminary and wholly insufficient nature. They are, however, factual and hence are recorded here. They do not represent a complete or systematic study of the various points under discussion, but since an examination of the literature shows a striking deficiency in knowledge regarding much of the physiology of tortoises, it is believed that these observations are worthy of record. In the two series of 1915-1917 and 1930 different points of view prevailed. The 1915-1917 series was obtained when the investigation was first started, but no extensive analysis of the findings was made at that time. The second series was obtained after the results of the first series had been sufficiently analyzed to indicate the obvious lacunæ. Furthermore, the technique later developed in the Nutrition Laboratory permitted certain observations that could not have been made in 1915. These may at first sight appear to be somewhat extraneous to our main thesis, that is, the respiratory metabolism of the tortoise, but it was deemed a justifiable expenditure of time to secure any observations that would throw light upon the nature of their metabolic processes.

From a preliminary survey of the metabolism of the tortoise, which was found to be much higher than that of other cold-blooded animals, it was thought that possibly this animal differed from other cold-blooded animals in having a body temperature somewhat or considerably above the temperature of the environment. A careful study of the rectal temperature compared with the environmental temperature was therefore made during the 1930 series. A few, although by no means carefully worked out, observations on the respiration rate and the insensible perspiration were also made. The excised turtle or tortoise heart has been used a great deal as a physiological preparation, but no records were found of the heart rate of the intact animal. Electrocardiograms were therefore obtained of tortoises Y and Z, to determine whether the heart rate is an index of the changes in metabolism under different conditions. A study of the character of the urine during the period of transition from full feed to prolonged fasting was also carried out, although it was impracticable to make

any quantitative analysis of the urine. Fragmentary notes regarding the feces were likewise secured. In view of the supposed importance of knowing the surface area of the tortoise and particularly the weight of the shell (to determine the weight less shell), one of the 1930 tortoises (Z) was killed at the end of the experimental series and the weight of shell as compared with the total weight was actually found. The ratio between its flesh weight and its shell weight was subsequently used in calculating similar ratios for the larger tortoises. Measurements of the shell itself and the skin area were likewise made.

With the tortoise, as with all animals studied in the Nutrition Laboratory, the goal was to secure information of any order that would ultimately throw light upon the processes of human physiology. The Nutrition Laboratory's studies on the comparative physiology of warm-blooded animals, ranging from observations on the albino rat to those on steers, have proved of great help, and it was in the belief that studies of the metabolism of cold-blooded animals would further illuminate the problems in warm-blooded metabolism that this investigation was undertaken. This is again another justification for recording all the carefully observed facts secured with regard to tortoises, even if they do not represent a complete study and their immediate relation to the metabolic research may not be obvious. Perhaps one of the most important functions of this investigation will be to emphasize further to zoologists and physiologists that careful studies of the so-called "cold-blooded" animals may aid in clarifying the various metabolic reactions of warm-blooded animals, since in the cold-blooded animal a distinctly unusual phase of the metabolic processes may manifest itself. Time and the pressure of other problems have made it impracticable to complete our original program, and the fact that not a little of this information has lain dormant for from ten to fifteen years before preparation for publication illustrates the difficulty of bringing the research to a satisfactory conclusion before this. In these records of the tortoise data, therefore, although it is hoped that the metabolism study is reasonably complete, it is realized that many of the observations represent only general hints or orientation studies of what probably are important physiological factors. In supplementing the 1915-1917 series by the 1930 series on tortoises while this monograph was being prepared, we simply yielded to an imperative need for further information on certain points that would make the interpretation of the earlier work clearer. But it is realized that these later observations only point out more definitely the insufficiency of the study as a whole.

### RESPIRATION RATE OF THE TORTOISE

The difficulty of determining the respiration rate of an animal when there is no material alteration in the rise and fall of the chest wall is obvious. The tortoise, however, appears to be a neck-breathing animal, that is, the neck seems to swell (although not a great deal) during breathing. With Y and Z in the 1930 series it was found that this periodic enlargement of the neck was particularly noticeable when the animals were immersed in warm water in a small air space, such as in the aquarium type of apparatus

shown in figure 10 (p. 33). The movements of the spirometer bell and the changes in the level of the float in the rotamesser attached to the respiration apparatus, when the tortoises were inside the respiration chamber, likewise gave some hint as to the probable respiration rate. Observations by these crude means showed that in general at an environmental temperature of 30° C. the tortoises breathed about two or three times each minute.

The mechanics of respiration of the tortoise have been discussed by Siefert.<sup>1</sup> The inspired air seems to pass only into the trachea and not into the lungs. Under such conditions, carbon dioxide would not necessarily be washed out from the lungs. There are also other animals, a certain species of frog, for example, that puff up in breathing, during which process the inspired air may not reach the lungs. It would be interesting to determine what is the air intake of the trachea of the tortoise and whether by this method of breathing it has a special means of inhaling dry air and exhaling it, saturated at its own body temperature, without lowering the alveolar carbon dioxide.

#### HEART RATE OF THE TORTOISE

It is believed that the heart rate of the tortoise may furnish a significant hint as to its metabolic activity. The heart rate of the tortoise can be measured only by means of an Einthoven string galvanometer or a capillary electrometer. Thanks to the technical skill of the physicist of the Nutrition Laboratory, Mr. V. Coropatchinsky, the heart rate of Y and of Z in the 1930 series was determined on a number of days, although not always under ideal conditions of muscular repose. The results are recorded in table 99, and two typical photographs of the galvanometer record are shown in figure 17 (p. 45).

Two electrodes, each consisting of several folds of fine brass mesh covered with thin cotton gauze and moistened with a normal saline solution, were attached to the tortoise by surgical plaster, one electrode being placed under one of the front legs where it joined the body and the other in a similar position under the diagonally opposite hind leg. With the electrodes in these positions the maximum electromotive force was obtained. When the electrodes had been adjusted, the animal was placed in a wooden box on the floor in a dark room. It soon sought a corner of the box and usually became quiet. Obviously a certain amount of disturbance to the tortoise was caused in handling it, to adjust the electrodes. Although the tortoise is singularly placid when compared with the irritable snake, it resents strict confinement such as was necessary for the measurement of the heart rate, and during these observations there were frequently active leg movements. It is always possible to distinguish between the photographic records of heart rate, which were especially characteristic, and the record of such leg movements. Only when the rate was especially slow, as during prolonged fasting or at low body temperatures, was it difficult to obtain a clear record of the heart beat. The environmental temperature recorded in table 99 is that at which the tortoise had been living just preceding the measurement of the heart rate. The animal was transferred from this

<sup>1</sup> Siefert, E., *Arch. f. d. ges. Physiol.*, 1896, **64**, p. 360.



environmental temperature to the room in which the galvanometer was located, and the records of body temperature and heart rate were obtained as soon as possible thereafter. The room in which the galvanometer readings were made had an average temperature of 23° C. The animal was wrapped in a blanket in being transferred to the galvanometer room, so

TABLE 99—Heart rate of tortoises Y and Z

Tortoise and date	Time	Hours fasting	Previous environmental temperature	Body temperature		Heart rate per minute
				Neck	Rectal	
1930			°C.	°C.	°C.	
Tortoise Y:						
Sept. 29....	2 <sup>h</sup> 30 <sup>m</sup> p.m.	240	22.3	23.30	.....	11.1
Sept. 29....	?	$\frac{1}{2}$	22.1	.....	.....	18.0
Oct. 6....	2 50	28	30.9	31.00	.....	26.5
Oct. 7....	9 26 a.m.	47	30.9	30.30	30.32	<sup>1</sup> 14.3
Oct. 8....	3 59 p.m.	77	31.6	30.10	30.28	<sup>1</sup> 18.6
Oct. 9....	4 34	102	30.3	30.48	30.40	<sup>1</sup> 17.1
Oct. 10....	3 00	124	31.7	30.55	30.72	12.6
Oct. 11....	4 36	150	....	30.65	31.10	18.3
Oct. 13....	3 04	196	29.9	30.14	29.68	16.3
Oct. 14....	9 20	226	....	29.51	29.40	17.0
Oct. 15....	4 15	245	29.5	30.00	29.30	18.6
Oct. 16....	3 57	269	30.0	28.80	.....	37.0
Oct. 17....	2 20	291	27.2	26.90	.....	12.4
Oct. 18....	4 25	317	29.4	28.20	28.38	15.3
Oct. 22....	8 47 a.m.	<sup>2</sup>	....	24.00	.....	15.4
Oct. 23....	2 53 p.m.	6	31.2	29.30	29.49	22.5
Oct. 29....	4 16	7	30.7	30.05	<sup>3</sup> 29.85	25.5
Tortoise Z:						
Sept. 15....	.....	100	....	.....	.....	<sup>4</sup> 43.6
Oct. 2....	4 57	24	31.5	29.50	.....	41.0
Oct. 10....	4 45	7	32.2	31.62	.....	35.5
Oct. 18....	4 50	49	28.9	28.50	.....	31.8
Oct. 27....	12 12	3	30.6	30.21	.....	52.0
Oct. 27....	1 55	5	<sup>5</sup>	<sup>5</sup> 20.30	.....	<sup>5</sup> 21.8
Oct. 28....	9 06 a.m.	24	14.1	<sup>6</sup> 13.71	13.33	9.3
Oct. 28....	2 50 p.m.	30	13.5	<sup>7</sup> 15.45	.....	10.9

<sup>1</sup> Restless.

<sup>2</sup> Had been eating each day for several days.

<sup>3</sup> Wet.

<sup>4</sup> Tortoise was on its back.

<sup>5</sup> Between 12.17 p.m. and 1.40 p.m. tortoise was in water, the temperature of which was gradually lowered from 29.1° to 14.8° C.

<sup>6</sup> 13.71° C. under hind right leg.

<sup>7</sup> 15.79° C. under hind left leg.

that it would not be exposed to a possibly lower temperature in the corridor. In all instances the heart beat was recorded about five minutes before the body temperature was obtained.

The records of heart rate shown in table 99 should be interpreted chiefly with reference to the body temperature of the tortoise. In the case of Y, with the exception of the high values of October 6 and 16, the heart rate at a body temperature of not far from 29° to 30° C. averaged 17 beats per minute, although the rate varied considerably with the length of fasting.

In the latter part of October, for example, when Y had received food, the rate was perceptibly higher even at the same environmental temperature. Measurements were not made with Y at very low body temperatures, the lowest being 23.3° C. on September 29, when the heart rate was 11 beats per minute.

With Z only one record of rectal temperature was secured, but the neck temperature was easily obtained. The heart rate of this tortoise was measured when the body temperature was at three different levels, at about 14°, 20° and 30° C. At these temperatures the heart rates averaged 10, 22, and from 31 to 52 beats per minute, respectively. The high value of 52 and the value at 20° were found but a short time after the tortoise had eaten. In general the heart rate, other things being equal, increased with the rise in body temperature.

Restlessness did not seem to affect the heart rate as much as one would expect. This is surprising, especially in view of the rapid paddling motions of both front and hind legs in those experiments when the tortoises were placed upon a stand so that the legs were unable to touch anything.

### BODY TEMPERATURE OF THE TORTOISE

In the preliminary survey of the metabolism data for the tortoises in the series of 1915-1917, the metabolism appeared to be high in comparison with that of the other species of cold-blooded animals studied. It was thought that if body-temperature measurements were available, this relatively high metabolism might be explained on the ground that the body temperature of the tortoise is appreciably above the temperature of the environment. The rectal temperature of the snake was found to be usually somewhat lower than the environmental temperature. These comparisons and the suggestion in the statement of Rubner<sup>1</sup> that possibly his tortoise studied at 20°, 30° and 37° C. did not follow the temperature of the environment made it incumbent upon us to secure information, in so far as possible, regarding the body temperature of the tortoise.<sup>2</sup> Hence in the 1930 series records were obtained of the body temperatures of Y and Z as often as possible, when the temperature conditions were sufficiently stable to make the measurements of any value. A mercurial thermometer was used in all cases.

The powerful muscles of the tail and those around the neck and legs made it difficult to secure the rectal temperature of these tortoises, although with Y this was frequently obtained. Tortoise Z resisted persistently and for the most part successfully any efforts to take its rectal temperature, and most of the rectal temperatures observed with this tortoise were secured on those days when the animal was definitely cold and hence less inclined to object to any insult. When the rectal temperature could not be taken, the thermometer was placed in the neck cavity formed when the

<sup>1</sup>Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 281.

<sup>2</sup>Examination of the literature shows extraordinarily few records of the temperature of these animals. One of the most recent reports is that of J. Cotte (*Compt. Rend. Soc. Biol.*, Paris, 1930, **104**, p. 1018) who, using a thermo-element, studied particularly the temperature reaction of tortoises when transferred from warm water to ice water. See likewise the report of Baldwin (*Biol. Bull.*, 1925, **48**, p. 432), who studied the relation of body to environmental temperatures in turtles.

tortoise drew its head into the shell, or it was placed in the front or rear groin in the cavity formed between the body and one of the front or hind legs. The environmental temperature was recorded with every possible precaution,<sup>1</sup> because of the desirability of securing an accurate observation for comparison with the rectal temperature of the tortoise and because of the significance of a difference of only a few tenths of a degree between the temperature of the environment and that of the tortoise.

The results are recorded in tables 100 and 101. Inspection of these tables shows that in general the temperatures of the neck and the groin agree well with the rectal temperature obtained at about the same time. Hence the rectal, neck and groin temperatures may be considered as having practically equal value. As a result of the experimental conditions planned for the different metabolism measurements, the environmental temperature at which the tortoises lived varied considerably, being as low sometimes as 14° and as high at other times as 31° or 32° and in one case as high as 36° C. With Y there was only a slight difference between the rectal and the neck temperature, the rectal temperature in general being possibly one-tenth of a degree higher. This was not invariably the case, for not infrequently it was about one-tenth of a degree lower. No direct comparison of the temperatures in the rectum and the groin is possible with Y, since the measurements in the groin were taken for the most part before the observations of the rectal temperature were attempted. The rectal temperature of Y was in general slightly above the environmental temperature. The environmental temperature was usually found by reading the temperature of the air at the point where it left the respiration chamber (from which the tortoise was subsequently taken for the body-temperature measurements) and the temperature of the water bath surrounding the chamber. These two temperatures were averaged to give the environmental temperature. In those instances when the tortoise was not in the respiration chamber, but in a cage in the laboratory room, the environmental temperature was determined from the graphic record of room temperature as registered by a Tycos thermometer. Later experience in determining the environmental temperature of the python studied in 1931 shows that the point of outlet from the respiration chamber is not an ideal place to make a temperature reading. The finding reported above, therefore, that is, that the rectal temperature of Y was somewhat above the temperature of the environment, may not be looked upon as an established fact. It must be borne in mind that the differences in temperature often amount to but a fraction of a degree. It must also further be remembered that the body temperature, rectal, neck or groin, was usually taken after the completion of the metabolism experiments when the tortoise was removed from the res-

<sup>1</sup> The precaution shown by J. J. Walbaum (*Chelonographia, oder Beschreibung einiger Schildkröten*, Lübeck and Leipzig, 1782, p. 26) in comparing the body temperature of the cold-blooded animal with the environmental temperature would have been well worth emulating by later writers. Walbaum speaks about the blood of a recently killed turtle being approximately 1° warmer than the atmosphere, but carefully points out that this difference may have been due to the lukewarm water in which the animal was kept for some little time before being killed, and emphasizes that this point with regard to the difference in temperature must be settled by making many experiments with turtles that have just been taken from the ocean.

TABLE 100—*Body temperature of tortoise Y compared with environmental temperature*

Date	Time	Hours fasting	Environmental temperature	Body temperature	
				Rectum	Neck or groin <sup>1</sup>
1930			°C.	°C.	°C.
Sept. 8	3 <sup>h</sup> 55 <sup>m</sup> p.m.	7	27.0	.....	26.80
Sept. 9	4 30	32	24.65	.....	25.38
Sept. 10	8 30 a.m.	48	23.20	.....	23.18
	2 08 p.m.	53	23.64	.....	23.99
Sept. 12	3 25	1	24.54	.....	24.68
	5 00	3	26.85	.....	26.02
Sept. 13	1 50	23	21.62	.....	22.23
	4 35	26	23.79	.....	23.61
Sept. 15	9 00 a.m.	66	ca.23	.....	23.49
	4 40 p.m.	74	25.62	.....	26.30
Sept. 16	8 55 a.m.	90	ca.24	.....	25.70
	11 15	93	24.25	.....	25.90
	2 35 p.m.	2	ca.26.5	.....	27.00
	3 55	4	25.29	.....	27.25
Sept. 18	12 35	0	26.2	.....	25.71
	3 35	4	23.9	.....	25.77
Sept. 19	2 40	1	25.4	25.50	.....
	4 40	3	24.39	25.30	.....
Sept. 20	8 30 a.m.	18	ca.23	24.21	.....
Sept. 22	8 30	66	ca.22.5	.....	22.90
Sept. 23	9 25	91	30.9	32.08	.....
	3 55 p.m.	98	31.25	31.62	.....
Sept. 24	9 00 a.m.	115	31.66	32.00	.....
	2 25 p.m.	120	31.03	31.70	.....
Sept. 25	9 20 a.m.	139	29.21	29.78	.....
Sept. 26	9 00	163	25.80	24.69	.....
	4 45 p.m.	170	16.65	17.80	.....
Sept. 27	8 30 a.m.	186	15.0	15.38	.....
	4 40 p.m.	194	17.27	18.85	18.55
Sept. 29	8 50 a.m.	235	.....	17.90	.....
	1 30 p.m.	239	22.31	21.44	21.45
	2 30	240	.....	.....	23.30
	4 30	242	22.10	23.70	23.50
Sept. 30	9 07 a.m.	259	ca.20.5	21.50	21.38
	4 47 p.m.	266	22.90	22.80	22.75
Oct. 1	9 05 a.m.	2	.....	30.80	30.60
Oct. 4	9 47	3	.....	28.78	28.60
	4 28 p.m.	3	33.01	31.95	31.85
Oct. 5	11 24 a.m.	0	.....	30.60	30.40
Oct. 6	8 45	22	30.76	31.58	31.40
	2 28 p.m.	27	30.85	32.00	31.93
Oct. 7	5 51 a.m.	43	30.91	31.42	31.02
	8 54	46	30.87	31.50	31.10
	9 26	47	.....	30.32	30.30
Oct. 8	8 57 a.m.	70	30.48	32.20	32.28
	3 38 p.m.	77	31.63	31.70	31.80
	3 59	77	.....	30.28	30.10
Oct. 9	8 40 a.m.	94	30.55	31.11	31.20
	4 10 p.m.	101	.....	31.52	31.55
	4 34	102	.....	30.40	30.48
Oct. 10	8 45 a.m.	118	31.72	32.88	32.80
	2 18 p.m.	123	31.69	32.20	32.00
	3 00	124	.....	30.72	30.55

TABLE 100—*Body temperature of tortoise Y compared with environmental temperature—(Continued)*

Date	Time	Hours fasting	Environmental temperature	Body temperature	
				Rectum	Neck or groin <sup>1</sup>
1930			°C.	°C.	°C.
Oct. 11	8 <sup>h</sup> 46 <sup>m</sup> a.m.	142	32.12	32.88	32.80
	4 18 p.m.	149	.....	31.95	31.90
	4 36	150	.....	31.10	30.65
Oct. 13	8 55 a.m.	190	32.68	34.35	34.50
	3 04 p.m.	196	29.92	29.68	30.14
Oct. 14	4 39	222	29.77	30.48	30.40
	9 01	226	.....	30.43	30.48
	9 20	226	.....	29.40	29.51
	9 33	227	.....	29.40	.....
Oct. 15	9 17 a.m.	238	31.79	32.50	32.53
	3 43 p.m.	245	.....	31.20	31.30
	4 15	245	29.5	29.30	30.00
Oct. 16	.....	.....	.....	31.00	31.05
	3 40	269	29.74	30.20	30.25
	3 57	269	30.04	.....	28.80
Oct. 17	9 58 a.m.	287	32.07	33.10	33.00
	2 02 p.m.	291	27.2	.....	27.80
	2 20	291	.....	.....	26.90
Oct. 18	9 06 a.m.	310	31.6	32.27	32.32
	1 48 p.m.	315	30.39	31.05	31.00
	4 11	317	29.4	29.80	29.58
	4 25	317	.....	28.38	28.20
Oct. 22	8 47 a.m.	<sup>5</sup>	.....	.....	24.00
Oct. 23	9 15	1	28.5	28.38	28.05
	2 32 p.m.	6	31.23	30.20	30.42
	2 53	6	.....	29.49	29.30
	4 50	8	29.2	29.60	29.50
Oct. 25	8 50 a.m.	48	30.37	29.60	28.70
Oct. 29	9 45	1	30.10	29.62	30.08
	3 52 p.m.	7	30.70	30.50	30.40
	4 16	7	.....	29.85	30.05
Oct. 30	8 55 a.m.	24	33.1	32.11	31.84
	12 00 noon	27	38.48	.....	35.66

<sup>1</sup> All observations between Sept. 8 and 22, incl., were taken in groin; the others were neck temperatures.

<sup>2</sup> Ate during night of Sept. 30-Oct. 1; exact time not known.

<sup>3</sup> Ate on Oct. 3; exact time not known.

<sup>4</sup> Determined after a respiration experiment, during which, especially toward end, there was a transition (increase) in environmental temperature.

<sup>5</sup> Had been eating for several days.

piration chamber into the environment of the laboratory room. This had two definite effects. On those days when the temperature of the respiration chamber was above that of the room, undoubtedly there was an opportunity for a rapid cooling of the tortoise. In the second place, there was on all days undoubtedly a struggle on the part of the animal which, judging from our experience with snakes, would tend to raise somewhat the body temperature. It is evident, therefore, that aside from the fact that the body temperature of the tortoise follows closely and rapidly the temperature of

TABLE 101—*Body temperature of tortoise Z compared with environmental temperature*

Date	Time	Hours fasting	Environmental temperature	Body temperature	
				Rectum	Neck or groin <sup>1</sup>
1930			°C.	°C.	°C.
Sept. 11	9 <sup>h</sup> 45 <sup>m</sup> a.m.	1	<sup>2</sup> 21.5	.....	22.11
	3 40 p.m.	6	26.86	.....	26.09
Sept. 12	8 35 a.m.	23	<sup>2</sup> 22.5	.....	23.68
	2 50 p.m.	30	27.30	.....	27.38
Sept. 13	8 50 a.m.	48	23.70	.....	24.59
	1 20 p.m.	52	24.20	.....	24.99
Sept. 15	9 00 a.m.	96	<sup>2</sup> 22.5	.....	23.72
	2 05 p.m.	101	24.71	.....	25.53
Sept. 16	2 10	125	24.75	.....	26.40
Sept. 17	9 05 a.m.	144	<sup>2</sup> 26.0	.....	27.00
	11 35	146	24.26	.....	26.70
Sept. 18	9 30	168	<sup>2</sup> 25.0	.....	26.58
	12 20 p.m.	171	24.02	.....	26.11
	4 13	175	25.88	.....	26.53
Sept. 19	11 45 a.m.	194	<sup>2</sup> 25.0	.....	25.35
	2 25 p.m.	197	24.24	.....	25.55
Sept. 20	8 48 a.m.	...	<sup>2</sup> 23.0	.....	24.42
	4 38 p.m.	223	26.52	.....	26.70
Sept. 24	2 45	28	25.0	.....	25.68
	4 45	30	24.05	.....	26.10
Sept. 25	3 05	52	<sup>2</sup> 25.0	.....	27.80
	4 45	54	26.28	27.20	.....
Sept. 26	10 00 a.m.	71	<sup>2</sup> 25.0	<sup>3</sup> .....	26.41
	4 10 p.m.	76	<sup>3</sup> 25.51	28.50	.....
Sept. 27	9 00 a.m.	94	25.62	25.71	.....
Sept. 29	8 30	142	<sup>2</sup> 17.0	17.30	.....
	4 35 p.m.	150	16.35	17.68	17.90
Sept. 30	8 45 a.m.	166	<sup>4</sup> 14.20	13.98	14.11
	10 25	168	<sup>5</sup> .....	17.50	17.92
	10 31 p.m.	168	17.60	17.70	18.00
Oct. 1	9 05 a.m.	<sup>6</sup> .....	<sup>4</sup> 14.80	15.15	15.20
	10 01	<sup>6</sup> .....	16.38	.....	16.68
Oct. 2	8 50	<sup>6</sup> .....	33.55	.....	34.84
	4 18 p.m.	<sup>6</sup> .....	31.54	30.45	30.70
	4 57	<sup>6</sup> .....	.....	.....	29.50
Oct. 3	9 50 a.m.	<sup>6</sup> .....	31.88	.....	32.51
	3 40 p.m.	<sup>6</sup> .....	32.53	30.48	30.30
	4 05	<sup>6</sup> .....	.....	.....	29.32
Oct. 9	8 40 a.m.	24	30.55	.....	32.23
Oct. 10	8 42	48	31.71	.....	33.74
	2 30 p.m.	5	31.0	.....	31.85
	4 30	7	32.20	.....	31.87
	4 45	7	.....	.....	31.62
Oct. 11	8 43 a.m.	23	32.12	.....	34.05
Oct. 18	9 04 a.m.	41	31.6	.....	33.10
	1 37 p.m.	46	29.60	.....	29.70
	4 50	49	.....	.....	28.50
	5 40	50	28.91	28.88	29.00
Oct. 24	.....	...	<sup>3</sup> 31.78	.....	32.42
Oct. 25	9 15 a.m.	0	<sup>4</sup> 30.37	.....	29.90
	1 22 p.m.	4	29.09	.....	30.20

TABLE 101—*Body temperature of tortoise Z compared with environmental temperature—(Continued)*

Date	Time	Hours fasting	Environmental temperature	Body temperature	
				Rectum	Neck or groin <sup>1</sup>
1930			°C.	°C.	°C.
Oct. 27	9 <sup>h</sup> 20 <sup>m</sup> a.m.	5 mins.	429.0	.....	28.40
	11 <sup>h</sup> 11	2	30.48	.....	30.60
	12 00 noon	3	30.55	.....	30.60
	12 12 p.m.	3	.....	.....	30.21
Oct. 28	9 06 a.m.	24	14.05	13.33	13.71
	2 34 p.m.	29	13.45	14.48	14.50
	2 36	29	.....	.....	14.38
	2 50	30	.....	.....	15.45
	2 55	30	.....	.....	15.79

<sup>1</sup> All the observations between Sept. 11 and Sept. 25 (3<sup>h</sup>05<sup>m</sup> p.m.), incl., those on Oct. 27 (5<sup>h</sup>08<sup>m</sup> p.m.), Oct. 28 (9<sup>h</sup>06<sup>m</sup> a.m.), Oct. 28 (2<sup>h</sup>36<sup>m</sup> p.m.) and Oct. 28 (2<sup>h</sup>55<sup>m</sup> p.m.) were taken in the groin; the others were neck temperatures.

<sup>2</sup> Environmental temperature increased somewhat from this level before body temperatures were recorded, as shown by graphic record of room temperature.

<sup>3</sup> Environmental temperature had fallen from about 28° at 10<sup>h</sup>06<sup>m</sup> a.m. to 25.51° at 4<sup>h</sup>10<sup>m</sup> p.m., when rectal temperature was taken.

<sup>4</sup> Temperature of water bath surrounding respiration chamber. Temperature of air leaving chamber not recorded.

<sup>5</sup> Environmental temperature increased between 8<sup>h</sup>45<sup>m</sup> and 10<sup>h</sup>25<sup>m</sup> a.m.; exact temperature not known.

<sup>6</sup> Ate on Oct. 1; exact time not known.

the environment (with the period of transition to be taken into account), little can be said with regard to the true difference between these two temperatures.

With Z fewer observations of the rectal temperature were available, although several were secured in the neck and the groin. Comparison of the measurements obtained in the neck and the rectum indicates that in general the temperature of the neck was slightly above that of the rectum. Comparison with the temperature of the environment shows, as with Y, that the body temperature of Z was usually slightly higher than the environment. The same criticism, however, applying to the measurement of the environmental temperature of Y holds here.

The effect upon the body temperature of the transition from a high to a low environmental temperature was studied in two instances. Thus, on September 26 tortoise Y was placed in the respiration chamber shown in figure 2 (p. 20), and the space between the outer and inner walls usually employed as a water jacket was packed with ice. At 9 a.m., when the temperature of the chamber was 25.80°, the rectal temperature was 24.69° C. Observations were made every half hour and, as will be seen from table 102, the body temperature decreased as the chamber temperature decreased. At 1 p.m., when the chamber temperature was 9.51°, the rectal temperature had fallen to 18.68° C. At 4<sup>h</sup>45<sup>m</sup> p.m., when the environmental temperature was 16.65°, the rectal temperature was 17.80° and the next morning,

September 27, the two temperatures were almost identical. On October 27, tortoise Z was studied in the respiration chamber during the morning at an average environmental temperature of 29° to 30°. Its neck temperature was 28.4°, 30.6°, 30.6°, and 30.2° during the morning between 9<sup>h</sup>20<sup>m</sup> a.m. and 12<sup>h</sup>12<sup>m</sup> p.m. At 12<sup>h</sup>17<sup>m</sup> p.m. it was placed in a water bath at a temperature of 29.1° C. The temperature of the water was lowered approximately one degree every five or ten minutes until, at 1<sup>h</sup>40<sup>m</sup> p.m., it was 14.8° C. As a result, the body temperature fell rapidly and, when the tortoise was removed from the water, the neck temperature was 18.40° C. The rectal temperature at this same time was 18.28° C. Temperatures in the front and rear groin were 17.21° and 17.49° C., respectively. At 1<sup>h</sup>55<sup>m</sup> p.m. the neck temperature was 20.2° C. All parts of the animal

TABLE 102—*Effect of falling environmental temperature on body temperature of tortoise Y, September 26*<sup>1</sup>

Time	Temperature of—	
	Environ- ment	Rectum
	°C.	°C.
9 <sup>h</sup> 00 <sup>m</sup> a.m.	25.80	24.69
9 30	19.06	24.11
10 00	14.32	23.81
10 30	12.86	22.21
11 00	11.01	21.09
11 30	10.00	20.30
12 01 p.m.	9.75	19.57
1 00	9.51	18.68

<sup>1</sup> Tortoise had been without food about 165 hours.

were wet at the time of these measurements. At 5<sup>h</sup>04<sup>m</sup> p.m., when the environmental temperature was 15.74° C., the temperature in the rear groin was 18.00° C. The next day, at 9<sup>h</sup>06<sup>m</sup> a.m., the rectal and groin temperatures were 13.3° and 13.7°, respectively, as compared with an environmental temperature of 14.1° C.

The general picture from these two series of observations on the effect of transition in environmental temperature is that the body temperature of the tortoise falls when the temperature of the environment is suddenly lowered, and becomes much the same as that of the environment when the environmental temperature stops falling and is held reasonably constant. Apparently, therefore, the tortoise forms no exception to the other cold-blooded animals in the reaction of its rectal temperature to that of the environment, since its body temperature tends to follow approximately the temperature of the environment. Hence a correct record of the environmental temperature under constant conditions is a reasonably true measure of the cell temperature of the tortoise, which, however, may be a few tenths of a degree higher or lower than the environment.



## INSENSIBLE PERSPIRATION OF THE TORTOISE

The water-vapor loss of tortoises has been the subject of a great deal of debate and has been especially considered by Krehl and Soetbeer, who argue that they found almost no water vaporized by this animal.<sup>1</sup> This curious belief in the absence of water vapor in the case of the tortoise is strikingly at variance with the experience of tortoise hunters.<sup>2</sup> Rubner, on the other hand, found a material loss of water vapor by the tortoise.<sup>3</sup> The output of water vapor can be measured in two ways. It can be directly determined, not by the use of hygrometers in the ingoing and outgoing air (which, in the experience of the Nutrition Laboratory, gives highly fallacious results) but by collecting and weighing quantitatively in suitable reagent bottles the water vapor in the air coming from the respiration chamber and by supplying dry air to the respiration chamber. Another method, which is for many purposes certainly helpful in indicating the trend of the water-vapor elimination, is to determine the insensible perspiration. The difference between the weight of oxygen inhaled by an animal and the weight of carbon dioxide exhaled (represented by the carbon of the organic material burned in the body and the organic hydrogen) is usually small, and it has been found that in general, certainly with humans, the insensible perspiration represents for the most part loss of water vapor. With warm-blooded animals also it has been the experience of the Nutrition Laboratory that the insensible perspiration is not only a measure of the water-vapor output, but likewise an index of the total metabolism. All these considerations led to the conviction that observations on the insensible perspiration of the tortoise were desirable, and since the technique employed with the tortoises was such that the water vapor itself could not advantageously be determined directly, a few experiments were accordingly made to measure the insensible perspiration. These were carried out with Y and Z.

The tortoise was placed in a wire basket and suspended on the arm of a Sauter balance of 10-kg. capacity, capable of weighing accurately to the nearest centigram. Owing to the passage of urine and feces following the ingestion of food, only three measurements were secured during the feeding period. The presence of either urine or feces complicates the determination of the insensible perspiration. One would expect that with the passage of excreta the measurements supposedly of the insensible perspiration would be exceedingly high, and it is only when very high values are found that the presence of urine and feces need be suspected. Regularity in the measurements of the insensible loss from hour to hour is excellent proof that the insensible perspiration alone has been measured. This was the case in all the observations carried out on Y and Z.

The records of insensible perspiration of Y, which may be considered to represent chiefly loss of water, are given in table 103; similar data for Z are presented in table 104. With Y on September 6 three periods of

<sup>1</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 626.

<sup>2</sup> Van Denburgh (*Proc. Calif. Acad. Sci.*, 1914, 4th ser., **2** (I), p. 218) states that the tortoise carries with it "a constant supply of water, in a bag at the root of the neck, which contains about 2 gallons."

<sup>3</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, pp. 280 *et seq.*

measurement, each of about one hour's duration when the animal was on full feed and when no feces or urine were passed, showed losses averaging 0.98 gram per hour. Unfortunately on this day the environmental temperature was not recorded, but in all probability it was not far from 22° C. This experiment is of interest chiefly in demonstrating the considerable amount of water that can be given off by an animal supposed by Krehl and Soetbeer to yield very little water. It also gives a hint as to the amount of insensible loss taking place during approximately the digestive cycle, for comparison with the losses found after long periods of fasting. In the later observations the environmental temperature, both dry bulb and wet bulb, was recorded. Previous to the measurements on September

TABLE 103—*Insensible perspiration of tortoise Y*

Date, environmental temperature, and days fasting	Rectal tempera- ture	Period		Insensible loss per hour
		Started at—	Length	
1930	°C.		<i>mins.</i>	<i>gm.</i>
Sept. 6:		1 <sup>h</sup> 49 <sup>m</sup> p.m.	62	0.97
Soon after food		2 51	61	.98
		3 52	62	.98
Sept. 29:	17.90	9 34 a.m.	83	.36
22.7° (dry bulb)		10 57	86	.42
13.2° (wet bulb)	21.44	12 23 p.m.	62	.39
10 days				
Sept. 30:	21.50	9 07 a.m.	62	.39
22.8° (dry bulb)		10 09	69	.36
13.2° (wet bulb)		11 18	59	.41
11 days		12 17 p.m.	76	.40
		1 33	56	.46
		2 29	67	.31
	22.80	3 36	65	.31

<sup>1</sup> Neck temperature was 21.45° C.

<sup>2</sup> Neck temperature was 22.75° C.

29 tortoise Y had been at a low environmental temperature of from 16° to 19°, and the rectal temperature at the start of the series of observations on this day was accordingly low, 17.90° C. Throughout the day the body temperature rose, however, and in the early afternoon was 21.44° C. The output of water vapor (as measured by the insensible perspiration) per hour, during three periods lasting somewhat over an hour each, averaged 0.39 gram, or considerably lower than that on September 6, but in the second experiment the tortoise had been fasting for 10 days. On the next day, September 30, tortoise Y was maintained at about the same temperature and was weighed at approximately hourly intervals throughout the day. The insensible loss averaged 0.38 gram. The insensible perspiration of this animal, therefore, when fasting about 10 days was less than half that taking place when it was on full feed. The environmental temperature was practically the same on the three days, and hence the difference in the insensible perspiration can not be explained by the temperature of the environment.

With Z the picture is much the same, although no experiments were made during digestion. On September 18 the temperature (dry bulb) of the room was 26° (wet bulb, 18.5°) and the body temperature of the animal was practically the same. Four periods of measurement showed an insensible perspiration amounting on the average to 0.44 gram per hour. At this time Z had been 7 days without food. On September 20 the environmental temperature was much the same as on September 18, but the body temperature was a little lower at the start. The insensible perspiration tended to increase throughout the day from 0.27 gram per hour in the morning to 0.53 gram in the early afternoon. The length of fasting was on the average 9 days. The tortoise was fed on September 21, 22 and 23, and the insensible perspiration was determined again on

TABLE 104—*Insensible perspiration of tortoise Z*

Date, environmental temperature, and days fasting	Neck tempera- ture	Period		Insensible loss per hour
		Started at—	Length	
1930	°C.		mins.	gm.
Sept. 18:	26.11	12 <sup>b</sup> 45 <sup>m</sup> p.m.	48	0.50
26.0° (dry bulb)		1 33	59	.41
18.5° (wet bulb)		2 32	56	.45
7 days		3 28	45	.40
Sept. 20:	24.42	8 48 a.m.	78	.27
26.6° (dry bulb)		10 06	78	.27
17.6° (wet bulb)		11 24	104	.39
9 days		1 08 p.m.	55	.53
		2 03	51	.53
		2 54	67	.45
	26.70	4 01	36	.49
Sept. 26:	26.41	11 27 a.m.	94	.84
27.2° (dry bulb)		1 01 p.m.	67	.72
21.1° (wet bulb)		2 08	60	.75
3 days	28.50	3 08	60	.62

<sup>1</sup>At 10 a.m.    <sup>2</sup>Rectal temperature.

September 26 when the animal had been about 3 days without food. The dry bulb temperature was practically the same as on the previous days, but the wet bulb temperature was a little higher. The insensible perspiration ranged from 0.84 to 0.62 gram per hour, or materially higher than the loss noted after 7 and 9 days of fasting.

It is clear from these observations (which fully confirm Rubner's findings) that the tortoise, although appearing to be very dry in comparison with the water turtle, does have a considerable water metabolism. This is shown not only by the marked increase in the body weights of Y and Z that took place within 24 hours after they reached the Nutrition Laboratory, following shipment from New York without food or water (see page 359), and by the fact that they frequently voided large quantities of urine, but also by the fact that there was a positive insensible perspiration, which was much larger during or near the time of digestion

than after prolonged fasting. Hence there is nothing in these results to suggest that the tortoise has an abnormal water metabolism or an abnormal reaction to the temperature of the environment. This is perhaps surprising, when one considers the large proportion of body area represented by the tough shell. But the shell itself can change its water content appreciably, as is shown by table 105 (p. 358). Thus, the shell of Z, immediately after the animal died and the flesh had been cleaned from the shell, weighed 1315 grams. In the course of ordinary drying in the laboratory the weight decreased to a minimum of 1152 grams. Without doubt, therefore, the shell participates somewhat in the insensible perspiration.<sup>1</sup> Indeed, there was a definite hint in our protocols that the shell changes its weight in part at least with the humidity of the air surrounding it. This is suggested likewise by the general structure of the shell. Furthermore, in some experiments made on insensible perspiration in which such irregular values were obtained that they have not been included in tables 103 and 104, it was found that the insensible loss per hour was somewhat less when the humidity was highest. The important feature of these observations, however, is not the exact quantitative relations between the insensible perspiration and the factors affecting it, but the established fact that the tortoise has an appreciable water metabolism.

Two reports by Maurel and de Rey-Pailhade<sup>2</sup> deal with the daily weight losses of the turtle, particularly with reference to environmental temperature. They noted great changes in the loss of weight at different temperatures.

### URINE OF THE TORTOISE

Supposing that the water metabolism of the tortoise was very low, we did not plan to make any study of the urine or attempt to determine the metabolized protein. Tortoises Y and Z passed urine from time to time when they were on feed and, usually, when the rectal thermometer was inserted, a few cubic centimeters of urine were passed. No definite information regarding the total amount of urine voided on any day was secured, but on four different days a sufficient amount of clear, uncontaminated urine was excreted by Y to enable a study of the reaction of the urine. In view of the interesting type of metabolism shown by the tortoises in the respiration experiments (subsequently to be discussed, pages 368 to 404), it is hardly necessary to emphasize the importance in any further investigation of this animal of a careful study of the urine. The tortoise is essentially a vegetarian, and obviously during a prolonged fast the character of its metabolism would be greatly changed from a combustion predominantly of carbohydrates to a combustion of fat and protein. Recalling the interesting research of Carpenter<sup>3</sup> on the composition

<sup>1</sup>Kayser (Ann. de Physiol., 1930, **6**, p. 724) assumes there is no loss of water through shell or skin of tortoise, but only through lungs.

<sup>2</sup>Maurel and de Rey-Pailhade, Bull. Soc. d'Histoire Naturelle de Toulouse, 1900, **33**, p. 246; *ibid.*, Compt. Rend. Soc. de Biol., 1900, **52**, p. 1061; Maurel, Compt. Rend. Soc. de Biol., 1900, **52**, p. 822.

<sup>3</sup>Carpenter, T. M., Proc. Nat. Acad. Sci., 1925, **11**, p. 155; Amer. Journ. Physiol., 1927, **81**, p. 519.

of steers' urine during prolonged fasting, we decided to study, with the kind aid of Dr. Carpenter, the reaction of the urine of Y on successive days during the progress of a fasting period. From the nature of the diet it was expected that the urine would be alkaline at the start and that, as the fasting continued, it would become strongly acid, as was the case with the steers. Apparently food is retained in the alimentary tract of the tortoise for a long time. Tortoise Y, for instance, passed feces weighing 19 grams when it had been fasting 4 days. It is possible that this long retention of food in the alimentary tract may contribute toward the formation of an alkaline urine. If so, the question arises as to whether the urine of the tortoise will change from alkaline to acid when the complete fasting stage is reached. So little is known with regard to the physiology of the tortoise in general that observations of this kind are well worth recording, even though few in number, as such information (along with the intermittent records of heart rate, insensible perspiration, and the like) helps to complete, in so far as possible, the picture of the physiology of the tortoise.

The indicators of Clark and Lubs, small quantities of which had been prepared for previous work in the Nutrition Laboratory, were used by Dr. Carpenter in the order of phenol red, cresol red, and thymol blue, to get an approximate indication as to the pH. On September 20, 1930, at 9 a.m., when Y had been 18 hours without food, this series of indicators showed that the urine had an approximate pH of from 8.4 to 8.8, that is, it was practically alkaline. A qualitative test with the S. R. Benedict solution indicated no sugar. On September 23 at 8<sup>h</sup>40<sup>m</sup> a.m., or 90 hours after food, the reaction of a specimen of urine of the same tortoise was equivalent to a pH of about 8.2, which was on the acid side of alkaline thymol blue and on the alkaline side of cresol red, that is, the urine was somewhat less alkaline than it had been on September 20. On September 24 at 3 p.m., or 120 hours after food, the reaction of the urine was alkaline to neutral litmus, alkaline to cresol red, and about the middle of the range of alkaline thymol blue. Indeed, Dr. Carpenter estimated that it was somewhat more alkaline than in the two preceding tests. On September 25 at 3 p.m., or 144 hours after food, the urine was distinctly acid to thymol blue alkaline, to cresol red, and also to phenol red. Only with brom cresol purple and brom thymol blue was it possible to obtain a relative (alkaline) reaction. The apparent pH was between 6.4 and 6.6. The urine 144 hours after food was therefore much more acid than any of the previous urines tested.

Thus, like the steer, the tortoise is a distinctly vegetarian animal with an alkaline urine when on feed, and when it reaches the stage of complete fasting it begins to subsist on body tissue and the urine becomes acid.

#### FECES OF THE TORTOISE

Since the tortoise supposedly is primarily a vegetarian, the fairly large mass of feces found in the box in which Y and Z were shipped to the Nutrition Laboratory was not at all surprising. In New York these tortoises had been fed chopped hay, and particles of this hay appeared in the

feces, apparently unaltered. The feces, on the arrival of the tortoises in Boston, contained a large number of small pebbles, like roofing gravel. At that time, unaware of the method of feeding the tortoises at the New York Zoological Park, we wondered whether these pebbles had been eaten as an essential factor of the digestive tract, comparable perhaps to the gizzard of a fowl. Information received later from Dr. Ditmars of the New York Zoological Park, however, indicated that from time to time small pieces of beef were thrown into the pen for the tortoises, the pen has a gravel bottom, and particles of gravel naturally adhere to and are eaten with the meat. This procedure accounted for the gravel found in the feces.

After Y and Z reached Boston they were fed lettuce and bananas, but had no access to gravel. On one occasion bananas were given with the skin on, and feces passed shortly thereafter contained intact pieces of banana skin. In view of the fact that the tortoise in the wild frequently subsists on cacti, for example, it is perhaps surprising that material as easily disintegrated, relatively, as a banana skin should have escaped the action of the digestive processes.

Another fact regarding the excreta is that even when the tortoises had been fasting many hours (91), rather considerable amounts of feces were passed. On October 16, when Y had been 267 hours without eating, it excreted two small pieces of feces.

On September 22 a large number of pebbles were found in the feces of Z, passed while the animal was on full feed. During the night of September 29-30, when it had been nearly 170 hours without food, feces were passed from which 5.3 grams of pebbles were washed out. Late in the afternoon of September 30, following the close of a metabolism experiment, feces were found in the respiration chamber containing 3.8 grams of pebbles. Again on October 1, feces appeared containing 9.2 grams of pebbles. Tortoise Z ate on October 1, but the time is not known. Since the tortoises arrived in Boston on September 5, it is seen that at least one of them continued to pass pebbles for nearly one month after leaving the New York Zoological Park, during which time it had had no possible access to pebbles. The retention of these pebbles in the alimentary tract for this length of time speaks for a digestive tract of extremely complicated mechanism, which should be given further anatomical study. During a considerable portion of this month, however, both tortoises and especially Z had been subjected to prolonged periods of fasting, which of itself would delay the passage of any inert material lodged at any point in the digestive tract.

## BODY MEASUREMENTS OF THE TORTOISE

### WEIGHT OF SHELL AND WEIGHT OF FLESH

Of all the animals studied by the Nutrition Laboratory during its investigations in comparative physiology, none presents a more singular proportion between seemingly inert and active body material than does the tortoise. Perhaps the stuffed goose, highly fattened, comes into this category, for its body weight includes a large proportion of fat which is commonly considered as metabolically inert. One or two of the obese subjects studied

by the Nutrition Laboratory may also come under this head, but that fat is entirely inert metabolically is by no means universally conceded. A large proportion, however, of the body weight of the tortoise is represented by its thick shell, which either is inert or has extremely little metabolic activity. The bones, because of their rich blood supply, probably play a much more active rôle in the metabolism than does the shell. Although it is known that the shell of the tortoise grows, it is commonly conceived from the nature of the shell that it is an inert mass that can not for a moment be compared with the flesh, from the standpoint of metabolic activity. In comparing the heat production of tortoises of different species and of the tortoise with that of the water turtle and other cold-blooded animals, and more especially in comparing the heat production of tortoises with that of warm-blooded animals, particularly man, it becomes important to make some correction for the weight of the seemingly inert shell. It was our good fortune to be able to measure the metabolism of a tortoise having a total body weight (132 kg.) nearly double that of the ordinary man and having a probable flesh weight, that is, weight less shell, much greater than that of the average man. It seemed desirable, therefore, to attempt to determine the relation between the weight of shell and the total weight of our tortoises or, in other words, to determine the flesh weight. Such information would not take into account the proportion of fat, water and protein, and the proportion of highly active material such as the large glands, but knowledge concerning the probable weight of flesh would enable more logical comparison of the tortoise's metabolism with that of other animals.

One might argue that the metabolism of tortoises of different weights could be compared on the basis of a unit of *total* body weight, but it is a well-known fact that the thickness of shell of these animals differs greatly. Although small tortoises can be killed and the differences in weight of shell and flesh studied, it is astonishing that the literature contains so few measurements of this sort.<sup>1</sup> Innumerable linear measurements of the shell and the head of the tortoise are recorded in the magnificent monograph of Van Denburgh,<sup>2</sup> but the only instances we have found of actually determined flesh or shell weights are the observations of Rubner and of Hall. Rubner clearly recognized the importance of considering, from the standpoint of metabolism, the weight less shell. He reports results on a tortoise that weighed after death 135 grams without the shell.<sup>3</sup> The total weight of his tortoise in experiments at 20°, 30° and 37° was 163, 156 and 149 grams, respectively. On the assumption that the tortoise died when its total weight was 149 grams, the weight of shell would be 14 grams, or 10 per cent of the total weight. Hall determined the shell weight of 14 different turtles ranging in weight from 19 to 470 grams and found that the shell constituted about 30 per cent of the total body weight.<sup>4</sup>

An attempt was made during the progress of our research to add to the meager information regarding the weight of shell of tortoises. At the Ameri-

<sup>1</sup> F. M. Baldwin (Amer. Journ. Physiol., 1926, **76**, p. 196), in reporting some observations on the metabolic rate of turtles, justly concludes that the shell and hard parts ("roughly one-third") should be deducted from the body weight.

<sup>2</sup> Van Denburgh, J., Proc. Calif. Acad. Sci., 1914, 4th ser., **2** (I), pp. 287 *et seq.*

<sup>3</sup> Rubner, M., Biochem. Zeitschr., 1924, **148**, p. 281.

<sup>4</sup> Hall, F. G., Journ. Metab. Research, 1924, **6**, p. 396.

can Museum of Natural History in New York a dead Iberian tortoise was dissected, and the following observations were obtained. The weight at death was 1324 grams. The shell with bones and skin weighed 527 grams. The bones that were not attached to the shell and the skin weighed 48 grams. On the assumption that the weight of shell would be represented by the difference between 527 and 48 grams, the shell weighed 479 grams or 36 per cent of the total weight. There is apparently an extraordinary difference between the proportionate weight of the inactive shell of the tortoise and the proportionate weight of the skeleton of the snake. Thus Dr. F. A. Lucas, Director of the American Museum of Natural History, New York, in 1917 kindly had the body of a rattlesnake (155 cm. long) subjected to peptic digestion and furnished us with the results of the test. The rattlesnake's total weight was 1939 grams and the skeleton weighed 205 grams, or slightly over 10 per cent of the total weight. In the case of the Iberian tortoise, if the weight of bones and skin were included with the weight of shell as inactive material (527 grams), 40 instead of 36 per cent of the total weight of the animal would be presumably inert material.

In 1915 Dr. F. S. Daggett, Director of the Museum of History, Science and Art at Los Angeles, California, published details regarding the body weight and body measurements of a Galapagos tortoise.<sup>1</sup> The Nutrition Laboratory corresponded with Dr. Daggett regarding the possibility of getting the weight of shell of this specimen and, thanks to his cooperation, weights were obtained of the mounted shell which indicated that its approximate weight was 30 kg. Undoubtedly since this specimen had been mounted for a long time, it had dried out considerably, and this would represent a minimum rather than a maximum weight. Since the animal weighed at death 204 kg., the shell represented nearly 15 per cent of the total weight. Obviously these gigantic tortoises are too costly to sacrifice and today, except for this one observation of Dr. Daggett, there is no definite knowledge regarding the relative weights of shell and flesh of the larger tortoises. The terrain over which the tortoises collected in the Galapagos and other islands must be transported after captivity offers so many difficulties that the preservation of the shell is usually considered the prime object, and consequently a study of the weights of different parts of the tortoise's body has thus far been wholly neglected.

When Y and Z were loaned to the Nutrition Laboratory by the New York Zoological Park, Dr. Ditmars kindly gave us permission to sacrifice one of them in order that the shell weight might be determined. Tortoise Z was accordingly killed at the end of the series of metabolism experiments.<sup>2</sup> The total body weight at the time of death was recorded, and the flesh and the bones were then separated from the shell. In dissecting this animal we unfortunately did not have enough experience to carry out the most satisfactory process recommended by Lucas,<sup>3</sup> but had to use the more simple method of boiling and mechanically removing as much of the flesh from the bones and shell as possible. The total weight of Z at death (Oc-

<sup>1</sup> Daggett, F. S., *Science*, 1915, n.s., **42**, No. 1096, p. 933.

<sup>2</sup> In the dissection of tortoise Z one large egg, nearly as large as a golf ball, and several smaller eggs were found.

<sup>3</sup> Lucas, F. A., *Proc. Amer. Assoc. Museums*, 1914, **8**, p. 151.



tober 29) was 3912 grams. The weight of the shell when the flesh and the bones had been removed varied considerably, according to the length of time after separation from the flesh, as the shell showed an obvious tendency to dry<sup>1</sup> (table 105). The first weight of the shell, 1315 grams, was determined on November 3, or five days after the death of the animal. Two days were occupied in boiling and removing the flesh. During the remaining three days the shell was left in the laboratory room, and the first weight was obtained only when there was no visible moisture on the shell. After the first three weights were secured, the drying process was hastened by placing the shell for a day or two (November 6 to 10) in an extremely

TABLE 105—Weights of shell of tortoise Z

Date	Time	Weight of shell	Date	Time	Weight of Shell
1930		gm.	1930		
Nov. 3	8 <sup>h</sup> 45 <sup>m</sup> a.m.	<sup>1</sup> 1315	Nov. 11	3 <sup>h</sup> 00 <sup>m</sup> p.m.	<sup>4</sup> 1265
Nov. 3	p.m.	1310	.....	4 00	<sup>5</sup> 1262
Nov. 5	4 30 p.m.	1261	.....	4 45	<sup>5</sup> 1259
Nov. 7	1 15	<sup>2</sup> 1211	Nov. 12	9 00 a.m.	<sup>6</sup> 1231
Nov. 8	4 45	1197	Nov. 13	11 45	1218
Nov. 9	4 30	1180	Nov. 14	1 00 p.m.	1213
Nov. 10	11 15 a.m.	1172	Nov. 15	11 30 a.m.	1209
Nov. 11	11 00	<sup>3</sup> 1289			
.....	12 00 noon	<sup>4</sup> 1275	1931		
.....	1 00 p.m.	<sup>4</sup> 1272	Jan. 12	p.m.	1155
.....	2 00	<sup>4</sup> 1269	Jan. 27	p.m.	1152

<sup>1</sup>Tortoise died Oct. 29.

<sup>2</sup>Shell in warm room from afternoon of Nov. 6 until 11 a.m., Nov. 10.

<sup>3</sup>Weight of shell after soaked over night in pail of water. Shell removed from water at 10<sup>h</sup>30<sup>m</sup> a.m., Nov. 11, and wiped nearly dry with towel. Shell wet inside.

<sup>4</sup>Shell damp inside.

<sup>5</sup>Shell appeared dry.

<sup>6</sup>Shell remained all day in warm air to dry, without any special air movement. After this, shell placed on top of balance in room and weights taken as shown on subsequent dates.

warm room through which ran the steam pipes for heating the Laboratory. During the night of November 10-11 the shell was soaked in water. On the morning of November 11 it was wiped nearly dry, and weights were obtained hourly between 11 a.m. and 4<sup>h</sup>45<sup>m</sup> p.m. These show clearly the effect of drying. From November 12 on, the shell was left in the ordinary air of the laboratory room and was weighed again from time to time between that date and the end of January. In order to calculate the weight of flesh of Z, the first shell weight determined after the animal's death, 1315 grams, has been accepted as most representative of the live shell weight. It has been assumed that this weight of shell did not alter materially during the two months of metabolism measurements preceding the death of the tortoise, and this shell weight may therefore be deducted from the total body weight to determine the flesh weight on any experimental day.

<sup>1</sup>Hall (Journ. Metab. Research, 1924, 6, p. 396) found that the loss in weight of the turtle shell is considerable, depending upon the size of the animal. With the larger turtles there was a loss of approximately 30 per cent in the weight of the shell, when it was dried.

Tortoises Y and Z were weighed frequently, as shown in tables 110 and 111 (pages 387 and 388), and the weights changed greatly throughout the short course of the experimental program. The animals were shipped from New York by express, and during transportation had been without water or food, other than a little hay. The first body weights determined immediately after they were taken out of the crate were strikingly low. Unfortunately these initial weights were not checked by a second observer, but it is believed that they are correct. At this time, *i.e.*, on September 5, tortoise Y weighed 4422 grams and tortoise Z, 3856 grams. Immediately after being uncrated they were given plenty of food, and water was accessible. On September 6, or 24 hours later, Y weighed 4763 grams and Z, 4366 grams, in the first case an increase of 341 grams and in the second case of 510 grams. In other words, the weights of these animals changed on the average about 10 per cent in 24 hours.

During September Z existed for the greater part of the time at an environmental temperature of about 25° C., and its total heat production per 24 hours under standard conditions at this temperature averaged not far from 13 calories. This would represent about 3 grams of dry protein or 12 grams of flesh (on the assumption that approximately 4 grams of water combine with every gram of protein to form flesh). Thus Z would have burned about 12 grams of flesh if it had burned pure protein each day. Our records show that not more than 48 hours elapsed between the time the tortoises left their feeding pen in New York and the time they were offered food in Boston. But even if the tortoise had received no food for four days before, it would hardly have burned 50 grams of flesh on this basis of calculation. If this amount is doubled to account for any activity the animal might have engaged in (although probably it was not active enough to account for a 100 per cent increase), there might have been a loss of flesh of 100 grams. Since Z gained 510 grams in weight in 24 hours when again given food, the increase in weight must have been due in greater part to water. It is believed that the water content of tortoise flesh is nearer 75<sup>1</sup> than the 60 per cent given for the average mammal. Consequently it would appear as if the normal water content of Z was more nearly represented by the body weights on September 6 and subsequent dates, when it was again on a normal feed level.

The body weights recorded after September 6 indicate that both tortoises had reached practically a constant weight level. The weights of Y were 4763, 5000, 4678 and 4536 grams on September 6, 8, 9 and 10, respectively, and those of Z were 4366, 4536, and 4479 grams on September 6, 8, and 10, respectively. In comparing the weight of shell with the total weight of Z to determine the weight of flesh, it is a question whether the initial weight of the animal when it arrived from New York should be used or the weight when it reached its weight level with food and water available, that is, a weight from 400 to 500 grams heavier. It was decided that the heavier weight included extra water, that this water was without doubt a part of the normal constituents of the body, and that the more representative value

<sup>1</sup> Rubner (*Biochem. Zeitschr.*, 1924, **148**, p. 281) states that there is 75.6 per cent of water in the flesh of the tortoise.

therefore would be that obtained when the animal was receiving food and water regularly and had reached a plateau in body weight. The average of the two weights recorded on September 6 and 8, 4451 grams, was therefore used for the purpose of this particular comparison, and it has been calculated that the shell weight of 1315 grams represents 29.5 per cent of this total weight. If the weight of the shell had been referred to the initial weight of 3856 grams on September 5, the percentage would be 34.<sup>1</sup>

In the computations later to be discussed (see page 388) of the heat production of Z per kilogram of flesh weight, the flesh weight was calculated on each experimental day by subtracting the actually determined weight of the shell, 1315 grams, from the total weight as measured on the day of the experiment.

The weights of the shells and the flesh weights of Y and of A to G in the 1915-1917 series were computed on the basis of the actual values found with Z. Tortoise Y was not killed but it was assumed, since it had received the same handling as Z and was probably in the same state of nutrition, that its shell weight would also be 29.5 per cent of its total weight when at the full feed level. The average weight of Y when on full feed was considered to be 4819 grams. The shell weight would therefore be 1422 grams. This weight of shell was subtracted from each of the daily weights obtained on the days of respiration experiments to secure the flesh weight for use in the calculations of heat production per kilogram of flesh weight. Since A to D, inclusive, of the 1915-1917 series weighed much the same as Z, that is, about 5 kg., it was considered that with these tortoises the shell would also weigh 29.5 per cent of the *initial* body weight. The shell weight as thus computed was deducted from the total body weights as recorded on the different experimental days, to obtain the weights of flesh. As a matter of fact, the body weight of A was not secured until it had been six days without food, when it was probably more nearly in the condition resembling that of Z on receipt at the Laboratory, and the percentage weight of shell would perhaps better be 34 rather than 29.5. The respiration experiments with B, C and D began in all cases 36 hours after food and hence it is believed that they were in a normal condition of weight. Consequently the weight of shell for all four of these tortoises has been considered to be 29.5 per cent of the initial weight, even though A presents somewhat of an exception. If the weight of shell for A had been calculated as 34 per cent of its weight rather than 29.5 per cent, the estimated weight of flesh would have been correspondingly smaller. Since the difference in flesh weight would be hardly 6 per cent, however, it has not been considered advisable to make this special calculation for A.

Although it seems justifiable to consider that the shell weights of the 5-kg. tortoises are equal to 29.5 per cent of their total weights, it is debatable whether this same percentage relationship holds with the larger animals. There is a striking lack of information with regard to the relationship between the total body weight and the weight of shell of the larger tortoises. The 204-kg. tortoise measured by Daggett (p. 357) had a thoroughly dried

<sup>1</sup> We also killed a small turtle (average total weight, 290 grams) and found that the shell weighed 79.2 grams or 27 per cent of its average weight (25 per cent of its maximum weight and 33 per cent of its minimum weight).

shell equivalent to about 15 per cent of its total weight or half the percentage found with our tortoise Z. This suggests that the percentage weight of shell does not remain constant as the body weight increases. It is impractical to kill an animal of this size and they die rarely, so that no definite information can readily be obtained other than this observation kindly furnished by Dr. Daggett. In the monograph of Van Denburgh<sup>1</sup> one finds the disconcerting statement that the shell, particularly of the larger tortoises, is thin and often comes off, and that ticks enter the cracks between the plastral plates, which would also suggest a thin shell. It is clear that the anatomy and structure of the shell and the body of the tortoise are by no means sufficiently well known. Rubner's small tortoise, as already mentioned, had a shell representing only about 10 per cent of its weight. Unfortunately the terms "tortoise" and "turtle" in English, to say nothing of other languages, are interchangeably used, as has been pointed out by Barbour in his admirable discussion of reptiles and amphibians.<sup>2</sup>

Although there is no definite information regarding the exact relationship between flesh weight or shell weight and the total weight with the giant tortoises, it is possible to arrive at the approximate percentage figure by attacking the problem from another point of view. On the assumption that the morphological law of growth shown by changes in the two-thirds power of the weight would represent changes not solely in the surface area of the flesh but likewise changes in the actual weight of the shell, an algebraic equation was formulated, based upon the shell weight and the flesh weight of Z, which were actually determined. According to this equation the two-thirds power of the flesh weight of Z is to the two-thirds power of the flesh weight of the large tortoise, whose total weight alone is known, as the actual weight of shell of Z is to X or the probable weight of shell of the large tortoise. Obviously the factor X, that is, the unknown weight of shell of the large tortoise, enters into both sides of the equation, for X must be deducted from the total weight of the large tortoise in order to obtain the flesh weight. In the case of tortoise G the equation is:  $3136^{2/3}:(132000-X)^{2/3}=1315:X$ .

The simplest method of solving such an equation is by trial and error, substituting various values for X in the equation until both sides of the equation work out alike. For G, weighing 132 kg., it was found that the value of X, that is, the probable weight of the shell, was 14.7 kg. This would correspond to 11 per cent of the total weight. A similar type of equation solved for E and F gave weights of shell of 9.4 and 10.4 kg., respectively. Since the total weights of these tortoises were 69.4 and 80.29 kg., the proportionate weights of shell represented 13.5 and 13 per cent of the total weights.

These calculations suggest that in general the larger the tortoise the smaller is the proportion of the total weight represented by the shell.<sup>3</sup> This conclusion seems at first sight inconsistent, when one recalls that

<sup>1</sup> Van Denburgh, J., Proc. Calif. Acad. Sci., 1914, 4th ser., 2 (I), p. 350.

<sup>2</sup> Barbour, T., *Reptiles and Amphibians*, Boston and New York, 1926, p. xviii, footnote 1.

<sup>3</sup> With snails Vernon (Journ. Physiol., 1897, 21, p. 460) found that the shell was 23 per cent of the total weight.

the 204-kg. tortoise measured by Daggett had a shell presumably weighing 15 per cent of its total weight. If, according to our calculations for Z, E, F and G, the percentage weight of shell decreases with increasing body weights, one would expect the shell of Daggett's tortoise to have represented nearer 10 than 15 per cent of the live weight. Since Daggett's shell had probably dried out considerably, this fact would increase the percentage. In any event, it is clear that the percentage of 29.5 found with the 5-kg. tortoise Z may not be applied in the case of the larger tortoises and, pending further information, we have used for E, F and G the computed weights of shell based upon the equation given above. These computed shell weights have been deducted from the total body weights at the time of the metabolism experiments, to obtain the probable weights of flesh. It is particularly unfortunate that this uncertain calculation must be used in order to compare the metabolism of the tortoises with that of the other cold-blooded animals that were studied. No other vertebrate is provided with such a large mass of inert material or material with such a low metabolic activity as is the tortoise. This fact, on the one hand, makes the tortoise extraordinarily interesting and important from the standpoint of comparative physiology and, on the other hand, it complicates the picture considerably.

#### SURFACE AREA OF THE TORTOISE

In his study of the heat production of different species of animals referred to body surface, Rubner had the problem of calculating the surface area of the tortoise. He determined the flesh weight of his tortoise and used this as the basis for the computation of the surface area, for this weight of flesh would correspond more or less to the weight of flesh of an animal not provided with a shell. Although the measurement of the shell area of the tortoise presents no insuperable difficulty, this measurement was not made by Rubner, for he argued that the mass of flesh less shell was of such a nature that the constant applicable, for example, to the two-thirds power of the weight of a frog could be applied equally as well to the two-thirds power of the weight less shell of the tortoise, in order to estimate the body surface. In our preliminary survey of the metabolism of the tortoises that we studied it was found that the heat production per square meter of body surface, when the body surface was computed by the use of the constant 4.62 suggested by Rubner,<sup>1</sup> did not approximate in any way that of the other cold-blooded animals. Hence it was concluded that either the constant 4.62 was too small or that this constant obtained on frogs did not apply to tortoises. Subsequently, in reviewing the literature on cold-blooded animals more thoroughly, we found that Fry<sup>2</sup> in 1913 had reported some important observations on frogs. Although Fry studied primarily the blood volume of frogs and lizards, he likewise included an extensive series of surface area measurements<sup>3</sup> of these animals. Twenty frogs ranging in weight from 3.5 to 36.9 grams were measured, and the

<sup>1</sup> Rubner, M., *Zeitschr. f. Biol.*, 1883, **19**, p. 553; *ibid.*, *Biochem. Zeitschr.*, 1924, **148**, p. 283.

<sup>2</sup> Fry, H. K., *Quart. Journ. Expt. Physiol.*, 1913, **7**, p. 185.

<sup>3</sup> It is regrettable that no hint of the presence of these careful measurements is to be found in the title to Fry's paper.

constant  $K$  averaged 11.2. Instead of applying this constant to the two-thirds power of the weight, Fry applied it to  $w^{0.68}$ , but this does not materially affect the comparison of the constant 11.2 with Rubner's original constant 4.62. Singularly enough, Fry makes no reference to Rubner's constant, although it differs so widely from his own findings. In 1930, Voit<sup>1</sup> published a series of measurements on the surface area of fish and frogs. He found the constant for frogs to be 10.88 and he computed from the body weight and the body surface of Rubner's frog that the constant should be 9.92 instead of 4.62.<sup>2</sup>

In the belief that the true constant is not far from 10, we have used a round figure of 10 for  $K$  in our calculations of the surface areas of our tortoises. It is debatable to what proportion of the total living weight of the tortoise this constant should be applied. Rubner deducted the weight of shell and from the flesh weight made his calculations of the surface area. The propriety of considering that the two-thirds power of the flesh weight of the tortoise times a constant  $K$  represents the surface area may be challenged. A large part of the tortoise is protected by the hard shell, the heat conductivity of which must be much lower than that of the flesh and from the surface of which relatively little water would be vaporized, except possibly for a slight vaporization between the plates. Nevertheless Rubner, who has had experience in this line of discussion vastly superior to all others, felt justified in using this method of calculation, and we have accordingly followed his plan with our tortoises. This is our justification for making the measurements and the assumptions with regard to flesh weights as outlined in the immediately preceding pages. The computation of the surface area of the tortoise is at best problematical and is complicated further by the difficulty of separating certain bones of the skeleton from the shell. It seems illogical to compute the surface area from the total weight or to include the area of an inert mass such as the shell. On the other hand, it may be argued that the cold-blooded animal has a body temperature essentially that of the environment and therefore, from the standpoint of any thermic law, the shell is as important a source of heat absorption or heat loss as would be the body denuded of the shell. In computing the surface area from the weight less shell, however, we are following strictly the procedure used by Rubner, who considered this the most logical method of attack in reporting his results for the tortoise. But in the case of his tortoise and in the case of our tortoise, Z, the weight of the shell was actually determined and the element of uncertainty in the calculation of the flesh mass did not enter. With the 5-kg. tortoises Y and A to D also it is believed that the flesh weight has been estimated without any appreciable uncertainty, but with the larger animals E, F and G, the calculation of the shell weight is open to question. Any error that enters into the calculation of the shell weight applies with equal force to the calculation of the surface area. It is believed, however, that any possible error in the calculation of the weight less shell is infinitely less significant than the possible error

<sup>1</sup> Voit, E., *Zeitschr. f. Biol.*, 1930, **90**, p. 237.

<sup>2</sup> See Pfaundler (*Zeitschr. f. Kinderheilk.*, 1916, **14**, p. 69) for further consideration of this error.

in the body-surface constant to be applied to this flesh weight. Rubner contends that the constant found for the frog may be used for the tortoise.

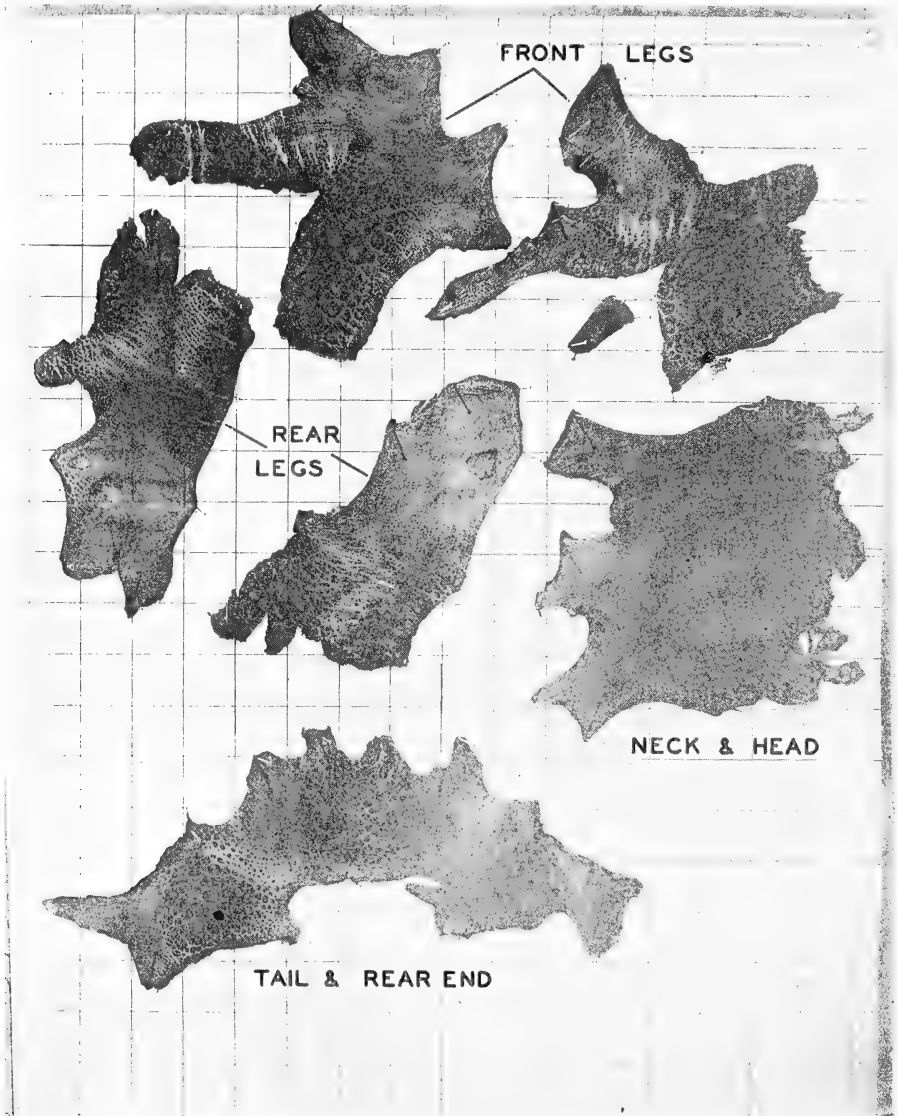


FIG. 85—PHOTOGRAPH OF THE SKIN OF TORTOISE Z.

Paper upon which skin is laid is ruled in square inches (equal to 6.5 square centimeters). Horny, scaly portions of skin were on more exposed surfaces of legs and tail; smoother portions were nearer to body inside shell.

Against this general thesis no criticism can be raised. But apparently neither Voit nor Rubner was aware of Fry's measurements of the surface area of the frog. The constant found by Fry is greater than either that reported by Voit or that computed by Voit from Rubner's original figures. It is ob-

vious, therefore, that the possible error in the constant  $K$  far exceeds the probable error in the computation of the weight of shell of the tortoise.

*Skin area*—A certain amount of the surface of the tortoise is represented by the skin, which is usually hard and horny but can be separated from the flesh on dissection. Tortoise Z was completely dissected in order to determine the flesh weight. In the dissection, the skin on the neck, head and legs was carefully removed, and, in so far as possible, any stretching was avoided. The different sections of the skin, as removed, were laid upon paper ruled in square inches, and a photograph was taken, as shown in figure 85. The skin had marked characteristics, depending upon what part of the body it came from, being extremely thin well up on the neck. Near the feet, on the other hand, the skin was horny, scaly and hard. The area of the skin was determined by measuring with a planimeter the areas of the different sections of skin in the photograph. It was found that the total skin area of Z, as thus measured, was 815 square centimeters. The surface area computed by means of the formula  $S=10 \times w^{2/3}$  ( $w$  being considered equal to the weight less shell), was close to 2000 square centimeters. The skin area, therefore, represented somewhat more than 40 per cent of the total computed body surface.

Since the tortoise can lose or gain considerable weight in spite of the rigid shell (Z, for instance, increased over 10 per cent in weight in one day—see page 359), it is a matter of speculation whether the so-called "surface area" undergoes any change commensurate with the change in weight. With the snake, the lizard, and the alligator the absence of shrinkage in skin with emaciation is obvious. It is possible that the cavities or recessions around the legs and the neck of the tortoise may account for the change in weight and the computed surface area. But since the rigid shell represents practically two-thirds of the total surface area and the skin area about one-third, it is difficult to conceive of any appreciable alteration in the total surface area with a change in weight. Hence the application of the surface-area conception to an animal of the anatomical structure of the tortoise seems questionable.

Whatever of value the calculations of the surface area of the tortoise may have from the zoological standpoint, the method adopted by Maurel and de Rey-Pailhade<sup>1</sup> is today more of scientific interest than importance, for they calculated by a complicated method the surface area of the shell itself. This was in turn referred to the body weight. But their method has no application to the problems in which we are especially interested.

#### MEASUREMENTS OF TORTOISE SHELL

In 1915 the importance attached by zoologists to measurements of the tortoise shell was not recognized by us, and no measurements were made of the shells of the tortoises in the series of 1915-1917. When the 1930 observations were in progress, opportunity was taken to measure the shell of the largest of the tortoises in the earlier series, G (132 kg.), which was still alive at the New York Zoological Park. The straight length of the

<sup>1</sup> Maurel and de Rey-Pailhade, Bull. Soc. d'Histoire Naturelle de Toulouse, 1900, **33**, p. 79.



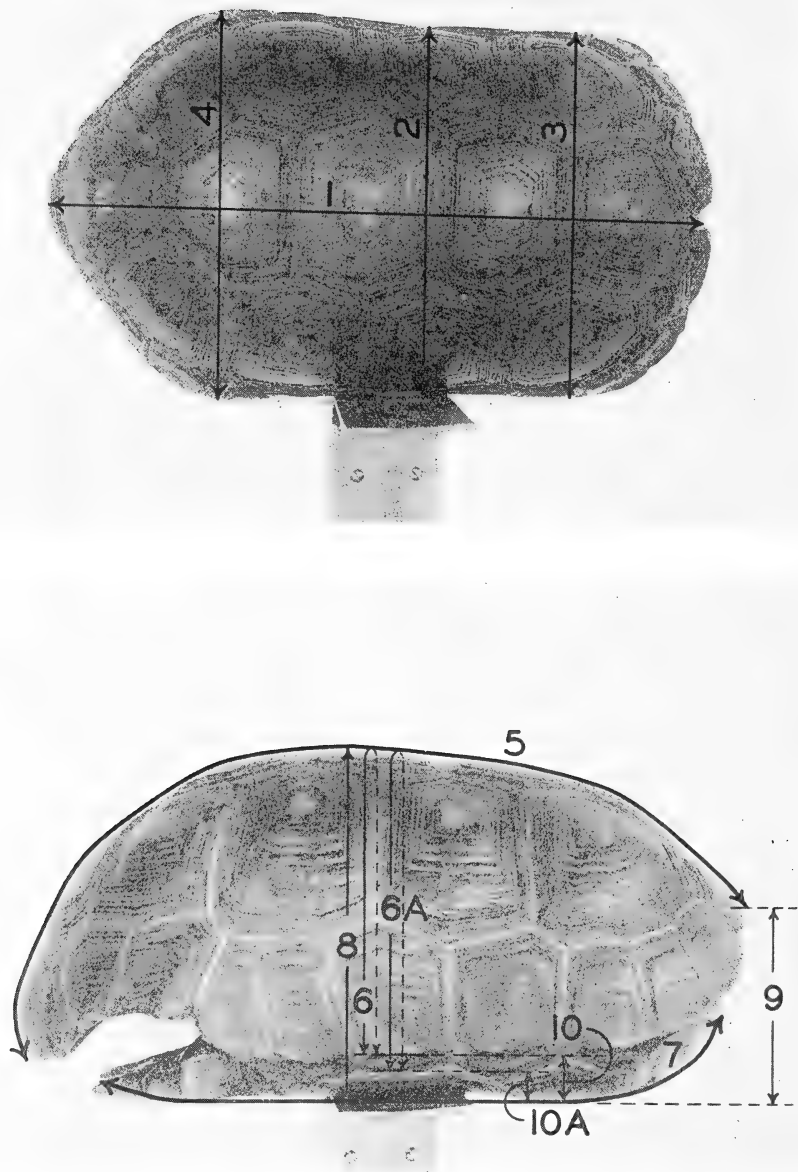


FIG. 86—LOCATION OF THE MEASUREMENTS OF THE TORTOISE SHELL.

Upper photograph indicates locations of straight measurements of length and width; lower photograph shows where measurements over carapace and measurements of height were taken. Paper used as a background is ruled in inch squares (25 x 25 mm.). This particular shell is shell of tortoise Z.

shell of G (as indicated by measurement 1 in figure 86) was 97 cm. and the over-all length or the distance over the curve of the carapace from tail to head (see measurement 5, figure 86) was 118 cm. Various methods have been adopted by zoologists to indicate the widths of the tortoise shell. The total straight width of the shell of G between imaginary perpendiculars touching the sides of the shell between the front and hind legs (measurement 2) was 76 cm. The width over the curve of the carapace (measurement 6) was 130 cm. Tortoise G weighed 138 kg. in 1928. There is no record of its weight since that time, but as the weight in 1928 is only 6 kg. greater than that in 1915, a small growth for a period of 13 years, it is

TABLE 106—*Measurements of shells of tortoises Y and Z*

Tortoise Y (Oct. 31, 1930)			Tortoise Z (Nov. 5, 1930)		
Location		Measure- ment	Location		Measure- ment
No.	Description <sup>1</sup>		No.	Description <sup>1</sup>	
		<i>mm.</i>			<i>mm.</i>
1	Straight length.....	306	1	Straight length.....	290
2	Straight width.....	180	2	Straight width.....	164
3	Front straight width..	179	3	Front straight width..	168
4	Rear straight width..	194	4	Rear straight width..	180
5	Length over curve....	407	5	Length over curve....	384
6	Width over curve....	339	6	Width over curve....	326
6A	Width over curve....	360	6A	Width over curve....	348
7	Length of plastron...	255	7	Length of plastron...	248
8	Middle height.....	146	8	Middle height.....	143
9	Front height.....	75	9	Front height.....	84
10	Height to marginals..	27	10	Height to marginals..	28
10A	Height to marginals..	16	10A	Height to marginals..	15

<sup>1</sup>Measurements made in accordance with description given by Lord Rothschild, *Novitates Zoologicae*, 1915, **22**, p. 403.

probable that the shell measurements obtained in 1930 are not far from those that existed in 1915. Ocular observations also indicate that G has not greatly changed its size since 1915.

Measurements of the shells of the other large tortoises were not taken, but a careful series was carried out on Y and Z in 1930. The results are recorded in table 106 and the exact location of the measurements is indicated in figure 86, which is actually a photograph of the shell of tortoise Z. It can be seen that these two tortoises were nearly of the same size, Z being slightly smaller than Y.

#### WEIGHT OF TORTOISE BONES

No analyses were made of the flesh of Z after it was killed, and therefore nothing is known regarding the percentage of dry matter, water, ash, etc., in its body, but the weight of the bones was determined. The bones were separated carefully from the flesh and the shell, although it is to be

noted that certain parts of the backbone are integral with the shell itself and can not be removed without destroying the shell.<sup>1</sup> The weight of the removable bones not permanently attached to the carapace was 93.58 grams. This weight was obtained on January 27, 1931, when the bones had been exposed to room air for nearly three months, and undoubtedly they had undergone desiccation similar to that represented so strikingly by the changes in the weight of shell shown in table 105 (p. 358). The bone weight of 94 grams, therefore, represents more particularly the true dry matter, although probably it still contained not far from 10 per cent of water.

The flesh weight of Z when on full feed has been estimated to have been 3136 grams. The 94 grams of bones represent 3 per cent of the flesh weight. It is interesting to compare this with the observations secured with a rattlesnake, the skeleton of which represented 10 per cent of its total weight or 12 per cent of its flesh weight. (See page 357 for details.)

## GASEOUS METABOLISM AND ENERGY TRANSFORMATIONS OF THE TORTOISE

### RESPIRATORY QUOTIENT

The relationship between the carbon dioxide produced or exhaled and the oxygen consumption has long been used as a general index of the character of the material metabolized. On the assumption that the carbon dioxide exhaled is a measure of the carbon dioxide produced and that the oxygen absorbed from the air is that actually consumed by the animal, such use of the respiratory quotient is justified. There has been no reason to suspect that with cold-blooded animals there would be any material alteration in the nature of the combustion of carbohydrate or fat. The nitrogen or the protein metabolism, on the other hand, undoubtedly is considerably different with snakes and birds, for example, than it is with mammals, since with the snake and the bird the end products of protein metabolism contain a large amount of uric acid, and the entire disintegration to urea and ammonia is not carried out. Rubner<sup>2</sup> has pointed out that there is no reason to suspect any peculiarities in the metabolism of fish and that even with the relatively fat-free fish that subsist a long time without food, the energy furnished by fat makes up a large proportion of their total metabolism.

With the large cold-blooded animals that we studied no attempts were made to determine the nitrogen metabolism, because of their irregularity in taking food, the difficulty of separating the urine from the feces, and the long intervals between the voidings of excreta. In the 1915-1917 series of experiments with tortoises the respiratory quotient was determined, but the results were so irregular and uncertain that it was believed to be unjustifiable to present them as representing true respiratory quotients. In

<sup>1</sup> H. Gadow (*Amphibia and Reptiles*, London, 1923, p. 328), in describing the tortoise, states that "the hard, firm carapace has partly rendered the supporting functions of the vertebral column unnecessary or impossible. In many tortoises, especially in the large land-tortoises, the vertebræ and the capitular portions of the ribs are reduced to mere bony outlines."

<sup>2</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 229.

general, the quotients were about 0.70 or 0.71, indicating fat combustion. In the 1930 series of experiments on the tortoise and in the 1931 series on the python the technique was modified (pp. 27 *et seq.*) so that the Carpenter gas-analysis apparatus could be used, and respiratory quotients were secured that must be accepted as technically correct. The respiratory quotients of the tortoise as obtained by means of the Carpenter gas-analysis apparatus, and these quotients alone, will be considered here. The respiratory quotients of the 1931 python are discussed on pages 407 to 418.

Since the tortoise is essentially a vegetarian and its food is chiefly carbohydrate, in contradistinction to the food of the carnivorous snake which is mainly protein and fat, one would expect that the respiratory quotient of the tortoise might be different from that of the snake, both during fasting and particularly during feeding. It was important, therefore, to determine the course of the respiratory quotient of the tortoise during the period of transition from maintenance on carbohydrate food to complete fasting, when the animal would be subsisting essentially upon fat. With carbohydrate-eating animals such as the goose or the pig, the transformation of carbohydrate into fat is usually studied by forced feeding. It was not practicable to feed the tortoise forcibly, and yet it seemed desirable to attempt to induce it to eat a sufficient amount of carbohydrate to throw light upon its capacity for converting carbohydrate into fat. Although in the natural state of living the food of tortoises, especially the large tortoises, is in large part certain species of cactus, the composition of which is unknown to us, nevertheless the body fat of the tortoise might be in part deposited from the food fat. The diet of the gopher tortoises living at the New York Zoological Park had been chiefly carrots, lettuce and bananas, that is, fat-poor material. In our 1930 experiments the tortoises received lettuce and bananas alone. It was quickly found that the bananas were untouched, if placed in the animal's cage whole, but if the skin were removed and the banana broken into 10- or 15-gram pieces, the tortoise would eat large amounts of it rapidly. Under ordinary conditions the tortoises ate about every other day, and if food were withheld for a day, they would frequently eat two or more bananas each the next day. Thus it was possible, without resorting to forced feeding, to secure observations on the respiratory quotient of this animal after a heavy carbohydrate-rich meal.

Data are available for both Y and Z. The *average* quotients obtained on the different experimental days are summarized in table 107. The actual measurements of the carbon-dioxide production and the oxygen consumption will be discussed later, when the gaseous metabolism and the heat production in general are considered (pp. 386 to 394). The average quotients only, as given in table 107, will be discussed here and not the period values, on the assumption that with the tortoise any change taking place in the character of the metabolism would be so slow that no material alteration could be expected in the respiratory quotient for a number of hours. Indeed, inspection of the period values in our original protocols has shown that as a rule the quotients are uniform from period to period on any given day, and that hence the averaging is justified. Averaging

the data means, however, that absolutely the highest and the lowest quotients found do not appear in table 107. Specifically, the maximum quotient found with Y was 1.39 on October 4 in the first period of the respiration experiment, 1½ hours after food. With Z the highest quotient was 1.47 in the sixth period on October 27, 7 hours after food. In those periods when the respiratory quotient was between 0.70, the quotient for fat, and 1.0, that for carbohydrate, the metabolism can not be suspected to have been abnormal. Quotients above 1.0 have frequently been found with warm-blooded animals when fed excessive amounts of carbohydrate. Such quotients have commonly been interpreted as an index of the transformation of carbohydrate into fat. The degree to which this transformation can progress is shown by the fact that with animals that lend themselves to forced feeding, notably the goose, respiratory quotients as high as 1.4 or over have been observed.<sup>1</sup> With the pig a high respiratory quotient has also been found in Lusk's laboratory, and a weak, emaciated dog (in which pancreatic external secretion was absent) having a severe disturbance of absorption of fat and protein was found by Pratt and his associate<sup>2</sup> still to be able to transform carbohydrates into fat, as indicated by respiratory quotients of 1.0 and above, although only slightly above 1.0.

With our tortoises there were only two average quotients below 0.70, namely, those for Y on September 15 and September 27. That on September 15 was 0.69. This, however, can hardly be considered as outside the range of experimental error. It is probably without any special physiological significance and indicates the metabolism of fat. Absolutely the lowest respiratory quotients were found with Y in the respiration experiment on September 27, when it had been almost 8 days without food. In this experiment the respiratory quotient in the first period was 0.61 and in the second period 0.59. These quotients were obtained when the environmental temperature was low, 18° C., and when the total metabolism was correspondingly low. On the day before, although the tortoise was also studied at 18°, two quotients were found about 7 days after food that were 0.73 and 0.75. These indicate nothing aberrant. On the days when Z was studied at a low temperature, September 29 and 30, and from 6 to 7 days without food, the lowest quotient was 0.72. It is believed to be significant that the low quotients found with Y occurred at a time when the environmental temperature was low. At the time of these experiments it was not clear, however, whether the results were to be explained by the low environmental temperature or the animal's low body temperature, or whether the extremely small amounts of gas involved in the determinations would introduce an experimental error. On the first day at the low temperature with Y (September 26) and on both days at the low temperature with Z (September 29 and 30, when the metabolism was at essentially a constant level) no difficulty was experienced in obtaining quotients inside the normal range.

Hall,<sup>3</sup> working with turtles, also found low respiratory quotients at low temperatures. His turtles weighed from 556 to 779 grams, and the en-

<sup>1</sup> Unpublished experiments of the Nutrition Laboratory.

<sup>2</sup> Morgulis, S., and J. H. Pratt, *Amer. Journ. Physiol.*, 1913, **32**, p. 200.

<sup>3</sup> Hall, F. G., *Journ. Metab. Research*, 1924, **6**, p. 393.

vironmental temperatures at which they were studied ranged from 0° to 29° C. At 29° the respiratory quotient was 0.76. Below 29° it was in all

TABLE 107—*Respiratory quotients of the tortoise*<sup>1</sup>  
(Average values)

Tortoise Y			Tortoise Z		
Date	Time without food	R. Q.	Date	Time without food	R. Q.
1930	<i>days hrs.</i>		1930	<i>days hrs.</i>	
Sept. 8	6	1.10	Sept. 11	4	1.17
Sept. 9	1 4	.85	Sept. 12	1 2	1.06
Sept. 10	2 3	.73	Sept. 13	2 3	.96
			Sept. 15	4 3	.75
Sept. 12	1	.86	Sept. 16	5 2	.72
Sept. 13	1 1	.82	Sept. 17	6 0	.75
Sept. 15	3 0	.69	Sept. 18	7 1	.73
Sept. 16	3 18	.73	Sept. 19	8 3	.74
Sept. 16	2	.74	Sept. 24	1 5	1.01
Sept. 18	3	1.08	Sept. 25	2 5	.87
			Sept. 29	6 1	.72
Sept. 19	2	1.18	Sept. 30	7 4	.80
Sept. 23	3 21	.79			
Sept. 24	4 20	.77	Oct. 2	2	.74
Sept. 25	5 21	.76	Oct. 3	2	.74
Sept. 26	7 0	.74			
Sept. 27	7 20	.60	Oct. 10	6	1.34
Oct. 4	3	1.35	Oct. 18	1 23	1.06
Oct. 6	1 0	1.13	Oct. 25	2	1.30
Oct. 7	1 20	.93			
Oct. 8	3 0	.81	Oct. 27	1	1.35
Oct. 9	3 23	.80	Oct. 27	6	1.36
Oct. 9	4 2	<sup>3</sup> .90	Oct. 28	1 2	1.21
Oct. 10	4 23	.84			
Oct. 11	6 0	.85			
Oct. 13	8 1	.73			
Oct. 14	9 7	.79			
Oct. 15	10 1	.75			
Oct. 18	13 0	.80			
Oct. 23	3	.96			
Oct. 29	<sup>4</sup>	1.22			
Oct. 30	<sup>4</sup>	1.30			

<sup>1</sup> Environmental temperature was between 23° and 31° in all experiments except on the following dates: Tortoise Y, Sept. 26 and 27, 18°; Oct. 30, 36°; Tortoise Z, Sept. 29 and 30, 17.8° and 17.6°; Oct. 27 (6 hrs.) 17°; Oct. 28, 14°.

<sup>2</sup> Ate on Oct. 1; time not known.

<sup>3</sup> Tortoise was active during determination of this quotient.

<sup>4</sup> Ate on Oct. 29; time not known.

instances lower than 0.70, ranging from 0.45 to 0.69. The turtles had all been fasting for over a week before the experiments, and Hall had the foresight to keep them for several hours prior to each experiment at the same temperature at which they were to be studied. Hall thinks the low quo-

tients may indicate the "formation of carbohydrate from fat, incomplete oxidation, or some other metabolic process of unknown nature." He also points out that "carbon dioxide may be stored in the tissues and the blood for some time, or it may be washed out of the lungs by ventilation in excess of the production."

Issekutz and Végh,<sup>1</sup> on the other hand, found high respiratory quotients with turtles at temperatures of from 18° to 20°. The turtles were caught in the fall and were studied during the winter, while fasting. The exact length of fasting is not stated. A turtle, weighing 1100 grams, had a respiratory quotient as high as 0.98 even on the tenth day of the respiration experiment during the fasting period. Another turtle, weighing 935 grams, had a quotient of 0.93 on the sixth day of the fasting experiment, and a third turtle, weighing 710 grams, had a quotient of 0.96 on the ninth day. These high quotients, which were likewise noted in subsequent periods extending over nearly two weeks, when the turtles were subjected to insulin treatment and were still fasting, were singularly constant throughout the entire series of observations. Practically all the quotients determined in the entire research lie within  $\pm 0.05$  of the quotient of 1.00. As a control on the apparatus, the authors cite five experiments with rats that had been fasting from 12 to 18 hours. The respiratory quotients of the rats were close to 0.78. It is difficult to understand these fasting quotients with the turtles of Issekutz and Végh, since they are invariably so much higher than those found with our fasting tortoises and those found by Hall with his turtles. The quotients in the rat experiments, although somewhat higher than the Nutrition Laboratory has found with rats fasting from 12 to 18 hours, were not unreasonably high and by themselves could certainly be taken as a satisfactory control of the apparatus. But it seems incredible that the respiratory quotient of the fasting turtle could be as high as 1.00.

A number of experiments have been made with regard to the respiratory quotient with some of the smaller cold-blooded animals, particularly the frog, when fed different foods. The difficulty of determining precisely the respiratory quotient of the frog can hardly be overestimated, owing to the small amounts of the gases to be measured and the possibilities for error, particularly in the measurement of the oxygen consumption. The data available on small cold-blooded animals, however, can not be discussed *in extenso* in this report. Respiratory quotients below 0.70 have been only too frequently reported in the literature, but it is highly probable that in the majority of cases they are the result of faulty technique. The low quotients found during hibernation and in diabetes are, however, of serious moment. In the case of hibernating animals extraordinarily low quotients have been reported, as low as 0.30. This is not the place to enter into a criticism of the technique employed when such low quotients were obtained, but they are not commonly accepted as a demonstration of a real change in body tissue. In the case of the diabetic patient, pages have been written discussing the difference between quotients of 0.71 and 0.69, and innumerable chemical formulæ representing the various partially oxidized products in protein and fat metabolism have been introduced to prove

<sup>1</sup> Issekutz, B. v., and F. Végh, *Biochem. Zeitschr.*, 1928, **192**, p. 383.

the possibility of such quotients. The low quotients have commonly been interpreted as indicating the transformation of fat into carbohydrate, that is, the reverse of the situation when high quotients are found. Needless to say, this interpretation has been strongly challenged, and the possibilities have been suggested of a markedly disturbed metabolism of all three food ingredients and, under certain experimental conditions, of the retention of carbon dioxide either by physical solution in the liquids of the body or by chemical absorption. This point will be discussed in more detail, when the respiratory quotients for the 1931 python are considered. (See pages 411 to 413.)

The gaseous metabolism experiments that were carried out in the aquarium type of respiration chamber (table 108) were accompanied by considerable activity. The tortoises were under distinctly unusual conditions in these aquarium experiments, and hence it is not strange that the quotients obtained do not always agree with the quotients secured in ob-

TABLE 108—*Respiratory quotients of the tortoise in "aquarium experiments"*

Tortoise and date	Time after food		R. Q.
	days	hrs.	
1930 Tortoise Y:			
Oct. 16	11	4	0.80
Oct. 17	12	2	.82
Oct. 18	13	4	.95
Oct. 23		7	.94
Tortoise Z:			
Oct. 18	1	20	1.03

servations immediately preceding but made with a different apparatus. These so-called "aquarium experiments" occurred with Y on October 16, October 17, October 18 (periods 3 and 4) and October 23 (periods 5 and 6), and with Z on October 18 (periods 1 and 2). On October 18 with Y particularly, the quotients in the two aquarium periods, 0.96 and 0.94, appear aberrant in comparison with the quotients of 0.80 and 0.81 in two immediately preceding periods obtained with a different type of respiration chamber (table 107).

The well-known influence of the ingestion of food upon the respiratory quotient<sup>1</sup> makes it imperative to consider all the respiratory quotients for Y and Z from the standpoint of the state of nutrition, with particular reference to the kind and amount of food eaten just prior to the measurement of the respiratory quotient and, to a certain extent, with reference to the amount of food consumed by the tortoises for several days preceding the test. Inspection of table 107 (p. 371) indicates that the average quotients ranged from 1.36 on October 27 with Z to 0.60 on September 27 with Y. In the first experiment with Y on September 8, a quotient of 1.10 was

<sup>1</sup>Chapman, H. C., and A. P. Brubaker (Proc. Acad. Nat. Sci., Phila., 1891, p. 13) found a respiratory quotient of 0.96 with a turtle studied after eating.



obtained 6 hours after food. The animal had been eating regularly lettuce and bananas. With many of the warm-blooded animals such as the Nutrition Laboratory has studied, the respiratory quotient 24 hours after food would be expected to be not far from that of fat. In this case 28 hours after food the quotient was still as high as 0.85. At the fifty-first hour it was down to that of fat. On September 11 Y received no food, but on the morning of September 12 it was offered food and ate almost constantly throughout the morning, consuming one head of lettuce and one banana and skin. One hour after the animal finished eating, the respiratory quotient was 0.86 or noticeably higher than the fat quotient on September 10. Thereafter the tortoise fasted until noon on September 16. The quotient was 0.82 even 25 hours after food, but had dropped to that of fat on the third day. On September 16 at 12<sup>h</sup>30<sup>m</sup> p.m. Y ate 222 grams of banana. Two hours later the quotient was still practically a fat quotient, and apparently the digestion was not rapid enough to increase the carbohydrate combustion. When studied on September 18 the tortoise had been feeding for two days on bananas, and on this particular day at noon had eaten an unweighed amount. Three hours later the respiratory quotient was 1.08. On September 19, a 110-gram banana was eaten and 2 hours later the quotient was 1.18. There then followed a fast lasting through September 27. From the third to the seventh day the quotient slowly fell until it reached a level characteristic of the combustion of fat. The extremely low quotient of September 27 has already been discussed. From October 1 to 4 the tortoise received lettuce and bananas regularly, consuming two bananas on October 2 and one banana on October 3. On October 4 it was placed in the respiration chamber with 93 grams of banana, of which it ate 40 grams. Three hours later the quotient was at the very high level of 1.35. Apparently the excessive feeding of carbohydrate for two days preceding had filled the glycogen reserves, and the excess amount of banana eaten resulted in the transformation of carbohydrate into fat.

On October 5 tortoise Y ate 104 grams of banana. On October 6 or 24 hours later the respiratory quotient was 1.13. The animal was then subjected to a 316-hour fast. After the surfeit feeding on October 1 to 4, when the quotient reached 1.35, the fall to the fat quotient was very slow, this level not being reached until 8 days after food. The quotient then increased to 0.80. The irregularities shown during this fasting period can not be explained by the technique and are difficult to explain from the standpoint of physiology. The first thought in looking at this series of quotients is that the fat metabolism 8 days after food has been supplanted by a protein metabolism. Tortoises as a rule are said to have a liberal supply of fat.<sup>1</sup> The fact that the larger tortoises, when on shipboard, have existed without food for as long as a year would imply that their protein reserve could not have been heavily drawn upon and that the 5-kg. tortoise, therefore, would draw even less heavily upon its protein reserve during a fast of only about 13 days. Yet the quotients around 0.80 found with Y after 8 days of fasting strongly suggest a protein metabolism. The impracticability of urine analyses at the time these observations were made

<sup>1</sup> Van Denburgh, J., Proc. Calif. Acad. Sci., 1914, 4th ser., 2 (I), p. 217.

deprives us of an important phase of this study. The lability of the carbon-dioxide excretion of these cold-blooded animals is such that one must have a much more open mind with regard to the shifts in the quotients than when one is dealing with warm-blooded animals. As yet the question of these respiratory quotients is distinctly unsettled. On the one hand, our experimental evidence seems to point clearly toward a quotient, 13 days after food, that would ordinarily be interpreted as indicative of protein metabolism. But the history of the long life of the tortoise without food would imply that their protein reserve is drawn upon only after a much longer fasting period than 13 days.

Tortoise Y was fed immediately after the termination of the experiment on October 18 and had free access to food and water. On October 22 it ate one banana, and at 9 a.m. on October 23 ate 150 grams of banana. Three hours later the average respiratory quotient was 0.96 and 4 hours later practically the same. After October 23 the tortoise ate regularly. On October 26 it ate three-quarters of a banana and some lettuce. On October 27 it ate 200 grams of banana and some lettuce, and on the morning of October 29 (exact time unknown) it ate 161 grams of banana. Shortly thereafter average quotients of 1.22 and 1.30 were found.

The general picture with Y is that the respiratory quotient is high following surfeit feeding of carbohydrate, and that during fasting after the ingestion of food it returns slowly to the fasting level, save in the long fast of October 6 to 18 when there was distinct evidence of a protein quotient after 8 days. Inasmuch as Y did not belong to the Nutrition Laboratory, we hesitated to subject it to a second prolonged fast to check this finding of a high quotient, for if the metabolism were approximating anything like a pre-mortal rise in nitrogen, it was not justifiable to risk the animal.

The respiratory quotients found with Z show much the same picture as those for Y. Prior to the experiment of September 11 tortoise Z had been eating bananas and lettuce regularly, although no record was kept of the exact amounts eaten. In observations extending over a period from 4 hours to 8 days after food, the respiratory quotient was found to be materially above 1.0 at the start. As the fast progressed, it fell to practically a fat quotient of from 0.72 to 0.75 and remained at that level for several days. Between September 20 and 24 food and water were given to the tortoise regularly, the last food eaten being 95 grams of banana at 11 a.m. on September 23. The next day, 29 hours later, the respiratory quotient was 1.01. Thereafter the values decreased. On October 1 (exact time not known) Z ate 1 banana and half a head of lettuce, but apparently this amount of food was not sufficient to increase the respiratory quotient, for on October 2 and 3 it remained at the fasting level. There was then a period of several days during which bananas were freely eaten. At 10 a.m. on October 10 the tortoise ate 83 grams of banana, and 6 hours later the quotient was 1.34. The animal was then fed again, the last feeding being on October 16 at 4 p.m., but the amount is not known. Forty-seven hours later, on October 18, the quotient was still slightly above unity. Thereafter, until October 25, the tortoise ate regularly, except on

October 23 when it refused food. At 9<sup>h</sup>15<sup>m</sup> a.m. on October 25 it ate 150 grams of banana and 2 hours later the quotient was 1.30. On October 26 it ate three-quarters of a banana and nibbled on some lettuce. On October 27 it ate a large amount of banana, 170 grams at 9 a.m. and 15 grams at 9<sup>h</sup>15<sup>m</sup> a.m. The respiratory quotient was accordingly very high (1.36) in the two experimental periods on October 27, and even when the animal had been 26 hours without food the quotient was still much above unity.

The picture with Z is much the same as with Y, except that the effect of fasting for 13 days was not studied and no real indication of a protein quotient following a fat quotient was obtained. Especially significant is the fact that values as high as 1.3 or thereabouts were found in a number of instances with Z, and in the last experiment on October 28, even 26 hours after food, the quotient was 1.21. It is clear that tortoises are capable of transforming carbohydrate into fat readily. Their metabolic needs, as will be seen later from a study of the gaseous metabolism (see pages 403 to 404), are low. The amount of food eaten at one meal by Y and Z was really several times their daily food needs and would supply them with a sufficient reserve to fill up the glycogen deposits and likewise permit the transformation of carbohydrate into fat.<sup>1</sup> It is striking that this cold-blooded animal with a very low metabolism should possess to such a high degree the capacity for converting carbohydrate into fat. When one considers that the tortoise can not be forcibly fed, it is even more surprising that its respiratory quotient after food ingestion should be essentially that found with the stuffed goose, with which surfeit feeding is possible.

#### EFFECT OF ACTIVITY ON GASEOUS METABOLISM OF THE TORTOISE

One of the prerequisites for basal metabolism measurements on men and animals, especially in comparative physiology where the results on one species of animal are to be compared with the results on another species, is that activity be ruled out as far as possible during the period of observation. This prerequisite differs markedly from the conditions stipulated by Rubner as essential for comparative metabolism measurements on various animals, since he used 24-hour periods and allowed what may be termed as "chamber activity." It was presupposed by us that these cold-blooded animals would present little difficulty from the standpoint of activity. Indeed, they are noticeably lethargic for the most part and, judging from visual observation, there would be practically no activity. As our results were accumulated, however, it became clear that whenever there was *any* activity, small though it seemed, there was frequently a pronounced effect upon the metabolism. Apparently following muscular activity of *any* kind there is an increase in metabolism which may be sustained for some time. The snakes, for example, although ideally quiet in nearly all the experimental periods, were found invariably to have a higher metabolism after they had been agitated or handled in being placed

<sup>1</sup>B. v. Issekutz and F. Végh (Biochem. Zeitschr., 1928, **192**, p. 385) found with normal turtles a blood-sugar content of 0.070 per cent and that the glycogen in the liver amounted to 10.63 per cent, values which indicate the relatively large carbohydrate storage of these animals.

in the respiration chamber (see pages 152 to 155). The 4-kg. alligator was so active that the observations with it were discontinued. With the lizards a few values were discarded because of activity, although in most cases the lizards were relatively quiet. With the tortoises great difficulty was experienced, especially in the beginning, in securing repose. Unfortunately many of the tortoise experiments at that time were considered of so little value that the weights of the carbon-dioxide absorbing vessels were not even recorded, and hence a valuable contribution to the metabolism of the tortoise during activity was lost. Among all our observations on tortoises there were, however, a sufficient number of instances in which the metabolism was measured during active periods to warrant consideration of the influence of activity upon the metabolism of this animal.

Tortoise D on February 23, in one period of 179 minutes, produced 0.586 gram of carbon dioxide per kilogram of body weight per 24 hours, at an environmental temperature of 22°. In a very active period on the following morning, at practically the same temperature, the carbon-dioxide production was 1.107 grams. Thus there was an increase in metabolism of nearly 100 per cent as the result of respiration chamber activity.

In the 1930 series, Y was quiet as a rule in all the experiments, save those in the latter part of October, when it was studied in the aquarium type of apparatus. There were considerable movements of the head and legs during the aquarium experiments and the periods of measurement in the aquarium were for the most part characterized by high metabolism. Thus, the highest average value recorded for the heat production per square meter of body surface per 24 hours for Y, unaffected by the ingestion of food, is 272 calories in the aquarium experiment of October 16 at 30° C. The next highest average value is 251 calories on October 9, when the tortoise was measured during two extremely active periods at a temperature of 29.8° C. At this time it had been 4 days and 2 hours without food. Since the standard heat production of Y at a temperature of 30° was about 80 calories per square meter of body surface per 24 hours (fig. 94, p. 392), it can be seen that the activity in these two instances increased the metabolism from about 200 to 250 per cent. This is an order of increment that with warm-blooded animals would have been accompanied by a great deal of external muscular work, and yet Y was able to engage only in "cage activity" consisting of movements of the head and legs. With Z there was no instance of such a high metabolism resulting from activity.

These percentage increments found with the tortoise are of a magnitude comparable to those found with snakes and bear out strikingly the conclusion that the cold-blooded animal may increase its standard metabolism by seemingly not excessive and apparently non-productive muscular work to a degree entirely outside the experience with warm-blooded animals in a respiration chamber.

#### STANDARD METABOLISM OF THE TORTOISES IN THE 1915-1917 SERIES

The results of the standard metabolism measurements on these animals (A to G), that is, the metabolism during periods unaffected by ingestion of food, by activity and agitation, or by transition in environmental tem-

perature, are recorded in table 109. The respiratory quotients, as shown in the first footnote in this table, represent assumptions of the most probable quotients of these animals according to the length of time that they had been fasting. These assumptions have been based upon the series of quotients actually determined for Y and Z (table 107, p. 371). The heat production has been computed from the carbon-dioxide production and its caloric value at these assumed quotients. The calcula-

TABLE 109—*Standard metabolism of tortoises in 1915-1917 series*

Tortoise and date	Time without food	Body weight		Periods		CO <sub>2</sub> per kg. (total weight) per 24 hours	Heat produced per 24 hours <sup>1</sup>			Environmental temperature
		With shell	Without shell <sup>2</sup>	Total number	Total length		Per kg.		Per sq. m. <sup>2</sup>	
							Total weight	Flesh weight <sup>3</sup>		
Tortoise A:										
Dec. 13, 1915.....	6 days	5.45	3.84	1	5	gm. 0.352	cal. 1.17	cal. 1.66	cal. 26.0	°C. 21.7
Dec. 14, 1915.....	7 days	5.45	3.84	1	5	.837	2.78	3.95	61.8	31.1
Dec. 15, 1915.....	8 days	5.45	3.84	1	6	.528	1.76	2.49	39.1	23.4
Dec. 16, 1915.....	9 days	5.45	3.84	1	6	.925	3.08	4.36	68.4	31.3
Dec. 17, 1915.....	10 days	5.45	3.84	1	7	.484	1.61	2.29	35.8	21.7
Dec. 18, 1915.....	11 days	5.45	3.84	1	6	.793	2.63	3.74	58.6	31.0
Dec. 19, 1915.....	12 days	5.45	3.84	1	6	.440	1.46	2.08	32.5	21.9
Dec. 20, 1915.....	13 days	5.45	3.84	1	9	.837	2.78	3.95	61.8	31.9
Dec. 21, 1915.....	14 days	5.45	3.84	1	16	.528	1.76	2.49	39.1	20.8
Dec. 22-23, 1915....	15 days	5.45	3.84	1	16	.881	2.93	4.16	65.1	30.3
Tortoise B:										
Aug. 8-9, 1916.....	36 hours	5.16	3.64	1	24	1.293	4.21	5.96	91.7	30.5
Aug. 11-12, 1916....	36 hours	5.16	3.64	1	24	1.250	4.07	5.77	88.7	30.5
Tortoise C:										
July 28, 1916.....	36 hours	5.87	4.14	1	3	.550	1.80	2.55	40.9	26.3
Aug. 8-9, 1916.....	36 hours	5.87	4.14	1	23	.681	2.22	3.15	50.5	28.2
Aug. 11-12, 1916....	36 hours	5.87	4.14	1	23	.595	1.94	2.75	44.2	27.7
Aug. 15-16, 1916....	36 hours	5.70	3.97	1	24	.607	1.97	2.83	44.8	27.9
Aug. 18-19, 1916....	36 hours	5.67	3.94	1	24	.540	1.76	2.54	40.0	28.0
Aug. 22-23, 1916....	36 hours	5.76	4.03	1	24	.450	1.46	2.09	33.3	23.3
Aug. 25-26, 1916....	36 hours	5.67	3.94	1	24	.353	1.14	1.64	26.0	23.0
Aug. 29-30, 1916....	36 hours	5.78	4.05	1	24	.239	0.78	1.12	17.8	18.0
Sept. 1-2, 1916.....	36 hours	5.76	4.03	1	24	.200	0.65	.93	14.8	18.2
Sept. 5-6, 1916.....	36 hours	5.84	4.11	1	21	.934	3.03	4.31	69.1	28.0
Sept. 8-9, 1916.....	36 hours	5.78	4.05	1	24	.711	2.31	3.30	52.5	28.0
Sept. 11-12, 1916....	36 hours	5.76	4.03	1	24	.877	2.85	4.07	64.7	31.6
Sept. 15-16, 1916....	36 hours	5.61	3.88	1	24	.807	2.63	3.80	59.7	31.8

tions of the weight less shell and the body surface have already been explained on pages 355 to 365. The values for the heat production per square meter of body surface of E and F, when studied together, have been based upon a summation of the body surfaces of the two tortoises as calculated separately from the computed "flesh weight" of each animal.

The chief feature of the 1915-1917 series of observations was not to study *in extenso* the metabolism of any one tortoise but to become oriented regarding the metabolism in general of the tortoise as a species differ-

TABLE 109.—Standard metabolism of tortoises in 1915-1917—(Continued)

Tortoise and date	Time without food	Body weight		Periods		CO <sub>2</sub> per kg. (total weight) per 24 hours	Heat produced per 24 hours <sup>1</sup>			Environmental temperature
							Per kg.		Per sq. m. <sup>2</sup>	
		With shell	Without shell <sup>2</sup>	Total number	Total length		Total weight	Flesh weight <sup>2</sup>		
Tortoise D:		kg.	kg.		hrs.	gm.	cal.	cal.	cal.	°C.
Feb. 20-21, 1917.....	.....	5.53	3.90	4	37	.533	1.73	2.45	38.6	18.3
Feb. 23-24, 1917.....	.....	5.35	3.72	3	19	.655	2.12	3.05	47.3	22.4
Tortoise E:										
Nov. 24, 1915.....	24 hours	369.40	60.00	2	3	.512	1.65	1.91	74.6	20.7
Nov. 25, 1915.....	48 hours	369.40	60.00	3	4	.439	1.41	1.63	63.9	21.7
Nov. 29, 1915.....	24 hours	369.40	60.00	2	5	.699	2.25	2.60	101.8	21.4
Nov. 30, 1915.....	48 hours	369.40	60.00	2	5	.436	1.40	1.62	63.5	19.6
Dec. 3, 1915.....	24 hours	369.40	60.00	2	5	.547	1.76	2.04	79.7	22.2
Dec. 4, 1915.....	48 hours	369.40	60.00	2	6	.405	1.30	1.51	59.0	21.9
Tortoise F:										
Nov. 22, 1915.....	24 hours	380.29	69.88	3	4	.520	1.67	1.92	79.2	19.9
Nov. 23, 1915.....	48 hours	380.20	69.88	4	5	.474	1.53	1.75	72.2	21.0
Nov. 26, 1915.....	24 hours	380.29	69.88	2	2	.606	1.95	2.24	92.2	21.7
Dec. 1, 1915.....	24 hours	380.29	69.88	2	4	.594	1.91	2.20	90.4	21.1
Dec. 2, 1915.....	48 hours	380.29	69.88	2	5	.454	1.46	1.68	69.1	20.2
Tortoise G:										
Dec. 8, 1915.....	54 hours	4131.5	116.8	5	6	.493	1.64	1.85	90.2	20.2
Dec. 9, 1915.....	78 hours	4131.5	116.8	4	5	.470	1.56	1.76	86.0	21.0
Tortoises E and F:										
Nov. 16, 1915.....	52 hours	149.7	129.9	3	4	.821	2.73	3.15	126.6	21.7
Nov. 17, 1915.....	71 hours	149.7	129.9	2	4	.726	2.41	2.78	111.9	24.4

<sup>1</sup> Calculated from carbon-dioxide production. Respiratory quotient of tortoises A, G, and E and F (studied together) was assumed to be 0.72; that of tortoises B and C, 0.74; that of tortoises D, E and F, 0.75.

<sup>2</sup> See explanation on pages 355 to 365 of method of calculating weight of shell and body surface.

<sup>3</sup> Weight determined on Dec. 14. <sup>4</sup> Weight determined on Dec. 7.

ent from the snake, the lizard and the alligator. The data for each tortoise will, therefore, not be considered separately, but the results as a whole will be analyzed. For this purpose the metabolism values for A to G, inclusive, have been plotted with reference to the environmental temperature, on the bases of the heat production per kilogram of total body weight (including shell), per kilogram of "flesh weight," and per square meter of body surface. The two observations obtained with E and F, when studied together, have also been included.

It will be noted from table 109 that the metabolism of E at 21° C., in the experiment of November 29, is much higher than its metabolism at the same temperature on other days. It does not seem justifiable to exclude this experiment from the table, however, since the carbon-dioxide production was measured in two consecutive periods (0.744 and 0.654 gram per kilogram of total weight per 24 hours) of 151 and 135 minutes, respectively, at a constant temperature of 21.4° C. Although every effort was made to secure adequate records of the degree of activity of these tortoises, it was possible for the functioning of the recording device to be easily disturbed by the movement of the large animal to one side of the chamber too near the knife edges, for example. But in order for this high metabolism to have been caused by activity, one would have expected that the tambour pointer would have moved sufficiently for the assistant to have recognized clearly the fact that the tortoise was definitely active. Indeed, this feature actually did occur in the first experiment with G, the largest tortoise, *i.e.*, on December 7. The results of this particular experiment with G are not, however, included in table 109.

#### STANDARD HEAT PRODUCTION PER KILOGRAM OF TOTAL BODY WEIGHT

In figure 87 have been plotted the values for the standard heat production per kilogram of total body weight per 24 hours of A to G, inclusive, referred to environmental temperature. A straight line represents probably as well as any form of curve the general trend of the metabolism. In this chart, as in some of the earlier charts shown for the boas, one sees that there is a definite individuality in the metabolism of some of the tortoises. Thus, the two points for B and those for D lie appreciably above the straight-line curve and all but one of the points for C lie below the curve. Another feature of this chart is that all the values for the giant tortoises E, F and G, group fairly closely about the general curve, although for the most part they are somewhat above the line. Thus it is seen that the larger tortoises have, if anything, a slightly greater metabolism per unit of body weight than the smaller 5-kg. tortoises. This finding is contrary to the general picture shown by warm-blooded animals that the heat production per unit of weight is lower, the larger the animal. With the snakes, on the contrary (p. 214), it was found that the 32-kg. python had a greater heat production per kilogram of body weight than the small Indian python during its long fasting period, although the 32-kg. python had been fasting for a longer period. This comparison of the effect of size upon the metabolism of the tortoise emphasizes the fact that, although with animals the composition of the body

as a whole is nearly the same whether they are large or small (with the notable exception of *fattened* domestic animals), the composition of the body of the 5-kg. tortoises (in so far as the relative proportions of weight of shell and total weight are concerned) differs greatly from that of the larger tortoises. In any consideration of the metabolism of tortoises of different size per unit of weight, therefore, the comparison is better made by taking into account the difference in the weight of shell.

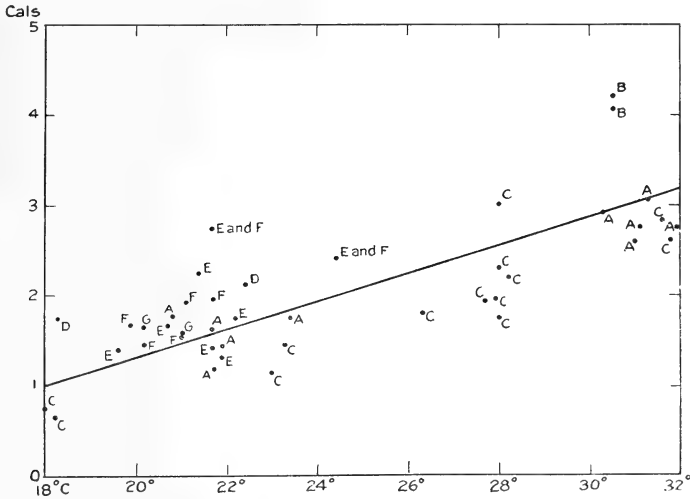


FIG. 87—STANDARD HEAT PRODUCTION PER KILOGRAM OF TOTAL BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISES A TO G.

Tortoises A to D, inclusive, weighed about 5 kg. each. Giant tortoises are represented by animals E, F and G.

#### STANDARD HEAT PRODUCTION PER KILOGRAM OF FLESH WEIGHT

The calculation for comparative purposes of the heat production per kilogram of total body weight of an animal such as the snake or the lizard or a warm-blooded animal has never been questioned, owing to the fact that the so-called "inactive" or bone tissue represents a relatively small percentage of the total body tissue and that the percentage of bone is approximately the same in all these animals. But with the tortoise, especially the thick-shelled land tortoise, the supposedly inactive bones and the shell make up not an inconsiderable proportion of its total weight. Since it is believed that the shell weights of tortoises differ greatly according to the size of the animal (pp. 360, 361), it becomes necessary, in order to compare the tortoise with other cold-blooded animals and with warm-blooded animals, to correct for the weight of shell. These corrections have been made according to the statement given on pages 360 to 362, and the results have been plotted in figure 88. Here again a straight-line curve seems to be best to indicate the general trend of the metabolism. Since the small animals each weighed about 5 kg. and the weight of shell was estimated to have been 29.5 per cent in each case, the relative positions of the plotted points for these tortoises (A to D) are much the same



in figure 88 as they were in figure 87, on the basis of total weight. The values for B and D are again characteristically high. The larger tortoises, E, F and G, varied in weight, the percentage weight of shell was not the same in all cases, and there has been a change in the positions of the plotted points for these animals in that they tend to approach a little more closely the curve indicating the general course of the metabolism, with a more even distribution of the points above and below the line. It may be concluded that the larger tortoises have about the same heat production per kilogram of body weight, when deduction is made for the weight of

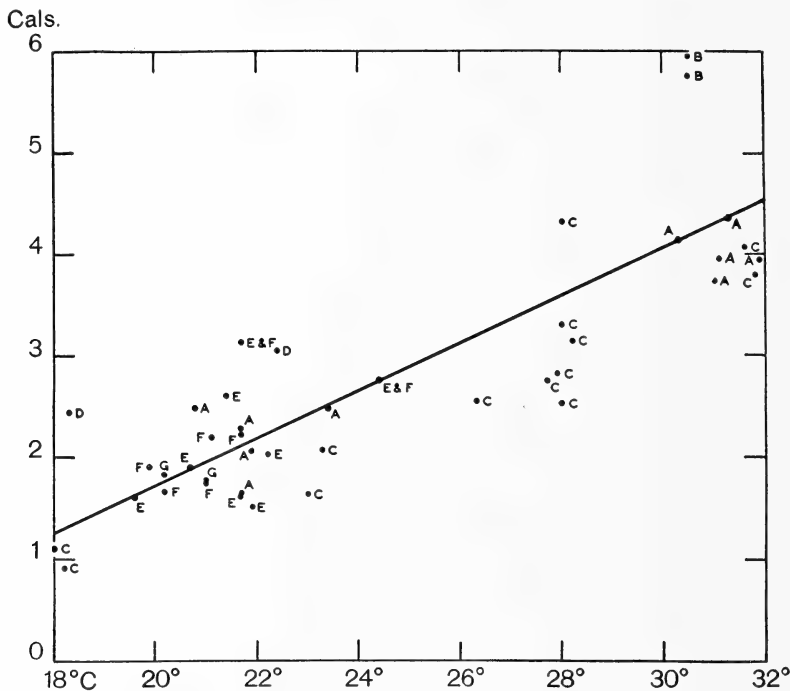


FIG. 88—STANDARD HEAT PRODUCTION PER KILOGRAM OF FLESH WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISES A TO G.

Tortoises A to D, inclusive, each weighed about 5 kg. (total weight). Giant tortoises are represented by animals E, F and G.

shell, as do the smaller ones. This is entirely at variance with the findings for warm-blooded animals. It would seem, therefore, as if with the tortoise a kilogram of flesh produces the same amount of heat, irrespective of size. The undesirability of subjecting the giant tortoises to higher environmental temperatures ruled out any study to determine whether this same relationship would hold true when the cell temperature of the tortoises approximated that of warm-blooded animals.

#### STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE

In order to present the results for the tortoises on the several bases of comparison commonly accepted among physiologists, the standard heat production has been computed per square meter of surface area. It is

recognized that in this calculation there is a possible error in estimating the flesh weight, but it is believed that this error can not be very serious. It is likewise recognized that the application of the constant 10 to the two-thirds power of the flesh weight may not be the best means of ob-

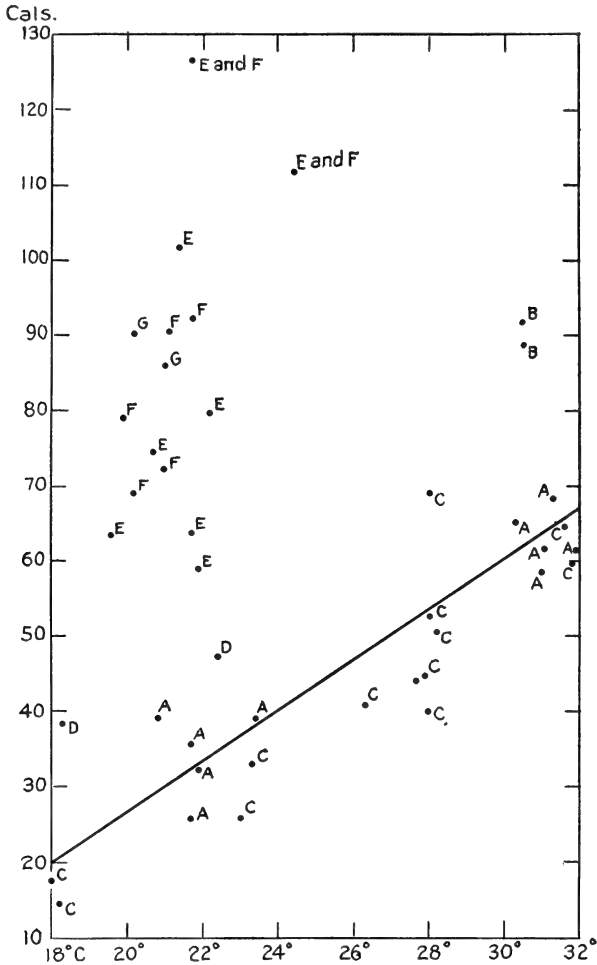


FIG. 89—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISES A TO G.

Tortoises A to D, inclusive, weighed about 5 kg. each. Giant tortoises represented by animals E, F and G. Straight-line curve indicates trend of metabolism only of 5-kg. animals.

taining the true body surface of the tortoise, but it seems to be the best procedure available at the present time. The results have been plotted in figure 89 with reference to the environmental temperature. Whatever the semblance of regularity in metabolism appearing in the charts for the snakes and lizards on the basis of surface area, there is no indication of

uniformity in heat production on this basis among the tortoises. To be sure, there is, as is to be expected, the same general distribution of points for the 5-kg. tortoises, A to D, inclusive, that was noted on the basis of total weight and of flesh weight. But the picture shown by the data for the larger animals, E, F and G, is incomprehensible. The plotted points for these three tortoises lie measurably above the points for the 5-kg. tortoises, and those for E and F, when studied together, lie inconceivably high. It has frequently been argued that the method of studying warm-blooded animals in groups tends to lower their metabolism. Recent experiments on sheep<sup>1</sup> and unpublished experiments on rats do not confirm this view. Snakes, when studied in groups, tend to coil in spherical form, but probably no animals could by nature of their structure be less adapted for huddling or close contact than tortoises. The proportion of the body surfaces that would come in contact with each other when two of these hard-shelled, semi-spherical animals are studied together in a respiration chamber would be insignificant. Hence, although E and F were studied simultaneously in two instances, the results can be considered not to be vitiated by any possible or theoretical disadvantage of a reduced surface area and reduced vaporization of water or loss of heat because of contact of the two animals.

There is nothing in the protocols to indicate any special reason for the high values for E, F and G, and it is clearly an established fact that the standard heat production per square meter of body surface, computed on the basis of shell-free weight, is extraordinarily high for these large animals. One is forced to the conviction that comparison of the metabolism of tortoises with reference to surface area has no significance whatsoever. It would be wholly unreasonable to attempt to lay any line through the plotted points in figure 89 to represent the general trend of the metabolism per unit of surface area of all these tortoises. This is particularly unfortunate, because such curves indicating with a fair degree of probability the trend of the standard metabolism per unit of surface area have been obtained for the snakes and the lizards. The most complete picture shown in figure 89 is for A and C, which were studied at frequent intervals over a wide temperature range. Tortoise D was measured only between 18° and 22° and B only at about 30° C. It might perhaps be logical to lay on a curve through the plotted points for the 5-kg. tortoises, A to D, and disregard entirely the data for the larger tortoises, and this accordingly has been done. The question then arises as to what is the average metabolism of the larger animals at 21° or 22°. The variation from any average value would be so great as to preclude using such an average as at all indicative of the probable metabolism of any individual giant tortoise at this temperature.

Since the calculation of the heat production per unit of body surface is supposed to equalize differences in size of animals, it is perhaps surprising that this discordant picture is obtained with the tortoises. It may be argued that the structure of the giant tortoise is entirely different from that

<sup>1</sup> Benedict, F. G., and E. G. Ritzman, *Wissensch. Arch. f. Landw., Abt. B., Tierernährung u. Tierzucht*, 1931, 5, p. 60.

of the smaller gopher tortoise. Certainly the thick shell, the dry skin, and the fact that they are land tortoises throws both the 5-kg. and the giant animals structurally and anatomically into much the same class, so that one would have expected the comparison of the metabolism of these different sized tortoises per square meter of body surface to be logical and justifiable. The striking difference between the level of the metabolism of the 5-kg. tortoises at, for instance, 20° to 22° and that of the giant tortoises leads one to wonder whether there is any relationship between the heat production per square meter of body surface and the size of the animal. In general, the values for E are lower than the values for F, particularly if the high value for E of 102 calories per square meter of body surface (commented upon on page 380) is omitted. The two values for G lie not far from those for F on the average, but the values for E and F, when studied together, are the highest of all. The weight of flesh of A to D averaged not far from 4 kg. each. That of E was 60 kg., of F 70 kg., of G 117 kg., and of E and F together, when averaged for one animal, 65 kg. So it is seen that the largest tortoise, G, although having nearly twice the weight of flesh of F, had a heat production per square meter of body surface on the average much the same as that of F, whereas E and F together, with an average flesh weight of only 65 kg. or about half that of G, had an enormously high heat production on this basis.

It is possible that we have here a real difference among animals of the same species, that is, that the larger tortoises have a greater blood supply than the smaller tortoises. The great difference in the metabolism of these tortoises suggests an intra-specific variation not found with the other species of animals in our series.

One might argue that these high values with the giant tortoises are due not wholly to physiological factors but to mathematical factors, and that if one knew the real body surface, the plotted points for the giant animals might more properly fall in line with those for the 5-kg. tortoises. The present calculations of the surface areas of the giant tortoises are based upon two assumptions, (1) that the shell weighs about 15 per cent of the total weight and (2) that the body-surface constant is 10. If this assumption were to be altered and the weight of shell were considered to be 30 per cent of the total weight, that is, the same as with the 5-kg. tortoises, such an increase in the weight of shell would decrease the calculated flesh weight. This, in turn, would decrease the surface area of the giant tortoise as computed by any method from the flesh weight and thus *increase* the heat production per square meter of body surface. The difference in metabolism per unit of surface area between the giant and the 5-kg. tortoises would then be even greater than it is now. If the body-surface constant, which has been assumed to be 10, were increased to 12.5, that used for the snake, this would result in an increased surface area which, in turn, would lower the calculated heat production per square meter of surface area. The change in the constant from 10 to 12.5 would, however, increase the computed surface area by only 25 per cent and the metabolism per unit of area would be lowered only about 25 per cent. If the metabolism of the giant tortoises at 21° were considered

from figure 89 to be, roughly, 85 calories per square meter of body surface, when the constant is 10, this could be lowered by changing the constant to 12.5 only to 64 calories. But the metabolism of the 5-kg. animals at 21°, which averages about 30 calories on the basis of a surface constant of 10, would also be lowered 25 per cent if the constant were changed to 12.5, so that the difference between the two sizes of tortoise would still be as great as now shown in figure 89. If the body surface calculations were altered, and the body surfaces of all the different tortoises were computed from the two-thirds power of the *total* weight (including shell) times a constant, even then the results for the giant tortoises would not be brought into line with those for the 5-kg. tortoises.

*Use of the general curves*—These curves for the tortoises and, indeed, the curves for the other cold-blooded animals, represent only the *general trend* of the metabolism per unit of body weight or body surface. Their chief value is not to predict the metabolism of an animal the weight of which alone is known, but as an index of the effect of differences in environmental temperature upon the metabolism. The metabolism of at least two of the tortoises, A and C, reacted to changes in environmental temperature essentially in accordance with the general curves for the other cold-blooded animals studied. But for the most part the variability in the data is too great to permit of using the curves as prediction curves. Indeed, it would be distinctly erroneous to use the curves to predict the metabolism of any given tortoise, as is clearly shown, for example, by the deviations from the curves of the plotted points for B and D.

#### INFLUENCE OF SEASON

It so happened that A and D were studied in the winter and B and C primarily in the summer. In view of the seasonal variability known to exist in the metabolism of cold-blooded animals, especially frogs, one might expect to find that season has an effect upon the heat production of the tortoise. Of the two tortoises studied during the winter, D is characterized by having standard metabolism values much higher than the general average. The plotted values for A, on the other hand, lie fairly close to the general average curves and at a definitely lower level than the data for D. Of the two tortoises measured during the summer months, B has a higher metabolism than C. Hence there is nothing in the results for either pair of animals to suggest a seasonal metabolism.

#### STANDARD METABOLISM OF TORTOISES IN THE 1930 SERIES

The three types of respiration chamber employed have been already described (see pages 27 to 33). The technique in the 1930 series of observations laid special emphasis upon the accurate determination of the respiratory quotient, and in this respect differed materially from that used in the earlier series. On the arrival of Y and Z in Boston on September 5, they were kept in a room at a comfortable temperature, not below 20°, and were fed lettuce and bananas, usually being given an unlimited supply. Prior to each respiration experiment careful note was made as to the kind and amount of food last eaten and the time when eaten, so

that the metabolism could be studied not only with reference to the environmental temperature but likewise with reference to the effect of the ingestion of food or of fasting. The average results of the standard metabolism experiments are summarized in table 110 for Y and in table 111 for Z. These averages represent periods of measurement with little or no activity, when the tortoises had been at least 24 hours and often longer without food, and when there was no sudden transition in environmental temperature. The body weight was determined on the day of each experiment. The weight of shell of Z was actually determined after its

TABLE 110—*Standard metabolism of tortoise Y*  
(Average values)

Date	Time without food	Body weight		Period		R. Q.	O <sub>2</sub> per kg. (less shell) per 24 hours	Heat produced per 24 hours			Environmental temperature
		Total	Less shell <sup>1</sup>	Total number	Total length			Per kg.		Per sq.m. <sup>1</sup>	
								Total weight	Less shell		
1930	<i>days hrs.</i>	<i>gm.</i>	<i>gm.</i>		<i>mins.</i>		<i>l.</i>	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
Sept. 9	1 4	4678	3256	9	400	0.85	0.865	2.94	4.23	62.6	24.9
Sept. 10	2 3	4536	3114	4	240	.73	.706	2.29	3.34	48.8	23.0
Sept. 13	1 1	4791	3369	3	120	.82	.889	3.03	4.31	64.7	23.0
Sept. 15	3 0	4451	3029	2	120	.69	.882	2.82	4.14	60.0	25.8
Sept. 16	3 18	4423	3001	1	120	.73	.886	2.84	4.18	60.3	25.6
Sept. 23	3 21	4423	3001	3	360	.79	1.232	4.01	5.91	85.2	30.0
Sept. 24	4 20	4366	2944	3	275	.77	1.170	3.76	5.59	80.2	30.1
Sept. 25	5 21	4479	3057	3	290	.76	1.090	3.55	5.20	75.5	30.5
Sept. 26	7 0	4423	3001	2	180	.74	.226	.73	1.08	15.5	18.1
Oct. 7	1 20	4451	3029	3	125	.93	1.270	4.28	6.28	90.9	30.2
Oct. 8	3 0	4394	2972	3	225	.81	1.148	3.74	5.53	79.6	30.4
Oct. 9	4 0	4337	2915	2	180	.80	1.013	3.28	4.88	69.6	28.3
Oct. 11	6 0	4309	2887	1	90	.85	1.160	3.79	5.66	80.5	29.6
Oct. 13	8 1	4281	2859	2	180	.73	1.042	3.29	4.92	69.9	29.2
Oct. 15	10 1	4252	2830	2	176	.75	1.254	3.97	5.96	84.3	28.7

<sup>1</sup> See pages 355 to 365 for explanation of method of calculating weight less shell and body surface.

death. The weight of shell of Y and the body surfaces of the two tortoises were calculated as explained on pages 355 to 365. The heat values are computed from the oxygen consumption and the caloric value of oxygen at the determined respiratory quotient. In the one instance (September 15, tortoise Y) when the quotient was below 0.70, the caloric value of oxygen was considered to have been that at the quotient of 0.70. No aquarium experiments have been included in the tables of standard metabolism data, because the tortoises were always active when in this type of apparatus.

The standard metabolism measurements on both animals reflect the influence of two factors, fasting and environmental temperature. Thus, the standard metabolism of Y was studied in September during a fast

lasting 7 days and again in October during a fast of 10 days. In the first fast the environmental temperature was held reasonably constant at from 23° to 26° C. through the ninetieth hour. It was then raised to 30° for the next three experiments and finally, on September 26, was dropped to 18° C. The effect of fasting is thus combined with the effect of differences in temperature. Since both fasting and environmental temperature have a profound influence upon the metabolism, it is difficult from the tabular presentation in tables 110 and 111 to study intelligently the

TABLE 111—*Standard metabolism of tortoise Z*  
(Average values)

Date	Time without food	Body weight		Period		R. Q.	O <sub>2</sub> per kg. (less shell) per 24 hours	Heat produced per 24 hours			Environmental temperature
		Total	Less shell <sup>1</sup>	Total number	Total length			Per kg.		Per sq.m. <sup>2</sup>	
								Total weight	Less shell		
1930	<i>days hrs.</i>	<i>gm.</i>	<i>gm.</i>		<i>mins.</i>		<i>l.</i>	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
Sept. 12	1 2	4139	2824	4	355	1.06	0.914	3.15	4.62	65.2	26.5
Sept. 13	2 3	4054	2739	4	240	.96	.731	2.47	3.65	51.1	24.0
Sept. 15	4 3	3941	2626	3	180	.75	.851	2.68	4.03	55.6	25.2
Sept. 16	5 2	3941	2626	1	120	.72	.915	2.86	4.30	59.3	26.1
Sept. 17	6 0	3912	2597	1	120	.75	.923	2.90	4.37	60.1	26.0
Sept. 18	7 1	3912	2597	2	120	.73	.820	2.57	3.87	53.2	25.2
Sept. 19	8 3	3827	2512	2	135	.74	.855	2.66	4.04	55.0	25.1
Sept. 24	1 5	4167	2852	2	80	1.01	.869	3.00	4.39	62.2	25.9
Sept. 25	2 5	4026	2711	2	90	.87	.859	2.83	4.20	58.5	26.9
Sept. 29	6 1	3685	2370	2	390	.72	.349	1.06	1.64	21.9	17.8
Sept. 30	7 4	3685	2370	3	652	.80	.344	1.06	1.65	22.0	17.6
Oct. 2	<sup>3</sup>	3657	2342	5	325	.74	1.124	3.40	5.32	70.6	30.3
Oct. 3	<sup>3</sup>	3629	2314	4	240	.74	1.038	3.13	4.91	64.9	29.9

<sup>1</sup> Shell weighed by actual determination 1315 gm.

<sup>2</sup> See pages 362 to 365 for explanation of method of computing body surface.

<sup>3</sup> Ate on Oct. 1; exact time not known.

effect of either factor upon the standard metabolism. It therefore seems best to plot the data in the form of charts and to analyze the results from the picture shown by these charts.

#### STANDARD HEAT PRODUCTION PER KILOGRAM OF TOTAL BODY WEIGHT

With an animal whose body weight ranges only from 4.7 to 4.2 kg., one might assume that the standard metabolism at different environmental temperatures could be satisfactorily compared on the basis of the total heat production per 24 hours. But since it is our object ultimately to compare the standard metabolism of the tortoises in the 1930 series with that of the tortoises in the earlier series, whose weights differed considerably, it seems best to refer the heat production to the time-honored units of body weight and body surface. The average values for the standard

heat production per kilogram of total body weight, including shell, have therefore been plotted with reference to environmental temperature in figures 90 and 91 for Y and Z, respectively. From these charts it can be seen that the majority of the measurements were made at temperatures above  $23^{\circ}$ , with one observation for Y and two for Z at  $18^{\circ}$ . The general trend of the standard metabolism of these two tortoises is probably best represented by a straight line. In this respect these two tortoises, as well as those in the 1915-1917 series, differ pronouncedly from the snakes and lizards, with which it was found that the average course of the standard metabolism was best indicated by a curving line, the upward inclination of which was much steeper at the higher than at the lower temperatures. A straight line perhaps does not fit the data for Z so well as for Y, for the plotted points suggest that the metabolism of Z was

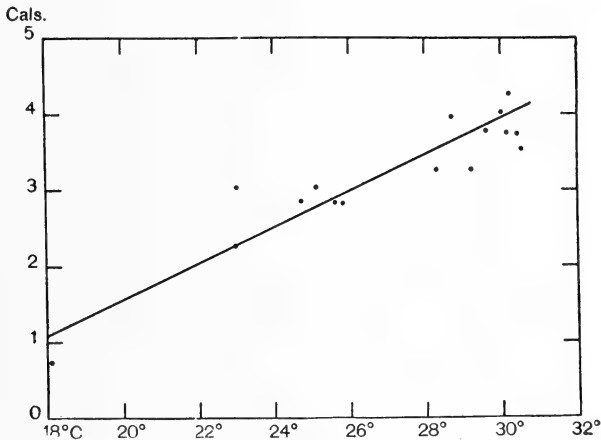


FIG. 90—STANDARD HEAT PRODUCTION PER KILOGRAM OF TOTAL BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISE Y.

practically constant between  $26^{\circ}$  and  $30^{\circ}$  C. This hint of a plateau in the metabolism of cold-blooded animals has been commented upon by Vernon,<sup>1</sup> but for the most part has been absent from our results. However, for purposes of general discussion and since tortoise Z was not studied at more frequent temperature intervals, a straight-line curve, representing its standard metabolism, has been drawn through the plotted points in figure 91 and a curved line has not been attempted.

Since Y and Z were of the same species, gopher tortoises, weighed approximately the same, and were subjected to the same treatment with regard to food, fasting and environmental temperature, it is possible to compare the metabolism of one with that of the other and determine whether they can be considered as physiological duplicates. The simplest method is perhaps to compare the two animals on the basis of the heat production per kilogram of total body weight. The two straight-line curves in figures 90 and 91 show that on this basis the standard metabolism of

<sup>1</sup>Vernon, H. M., *Journ. Physiol.*, 1894-1895, **17**, p. 277; *ibid.*, *Journ. Physiol.*, 1897, **21**, p. 443.



the two animals at the different environmental temperatures was much the same, the only significant difference being the two relatively low values at 30° with Z. Therefore these animals may well be considered to be physiological duplicates.

Judging from the curves for the standard heat production per kilogram of total body weight of Y and Z, one would assume that the temperature effect was a straight-line function and that the metabolism increases with the temperature. At 18° the metabolism would be about 1.0 calorie per kilogram of total body weight per 24 hours and at 28°, or 10 degrees higher, it would be approximately 3.5 calories. At the higher temperature the metabolism is thus 3.5 times that at the lower temperature, that is, there is an increment above the metabolism at 18° of 25 per cent per degree. This increment is not far from that found with many of the other cold-

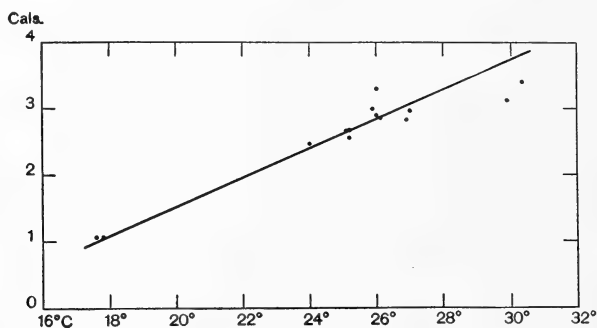


FIG. 91—STANDARD HEAT PRODUCTION PER KILOGRAM OF TOTAL BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISE Z.

blooded animals that we studied, although the shape of the curve for the tortoises is pronouncedly different.

#### STANDARD HEAT PRODUCTION PER KILOGRAM OF FLESH WEIGHT

Since the total body weight of the tortoise is comprised of a large mass of inert material, with probably a very low metabolism, the most logical method of comparing the heat production of these tortoises is to compute it per kilogram of body weight less the weight of the shell. The heat values thus computed have been plotted with reference to environmental temperature in figures 92 and 93 for Y and Z, respectively. These charts again show, as is to be expected, that the temperature effect is a straight-line function instead of a curved line. It is regretted that the metabolism of Y at 18° was not more definitely established. With Z there are two well-agreeing values at this temperature.

#### STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE

The surface area and the heat production per unit of surface area have been calculated for Y and Z and the heat values plotted with reference to environmental temperature, as shown in figures 94 and 95. In analyzing these charts, one should hold in mind the reservations already

pointed out in a previous section of this report (pp. 362 to 365) concerning the difficulties of estimating the true surface area of the tortoise. Here again with Y the single value at 18° introduces an element of uncertainty in the location of the line showing the general trend of the metabolism. If the line were drawn through the value at 18°, it would

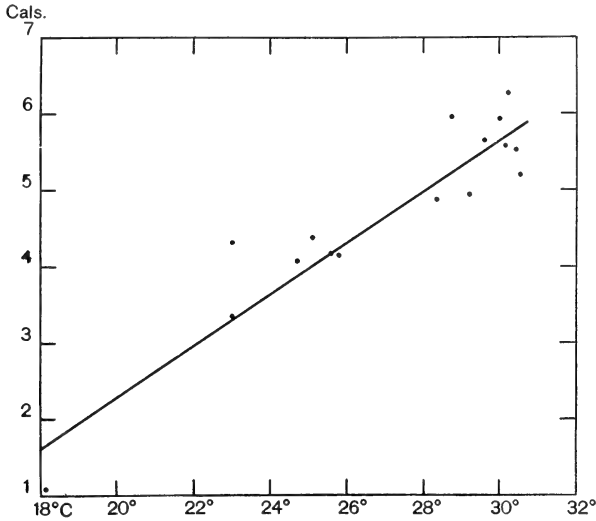


FIG. 92—STANDARD HEAT PRODUCTION PER KILOGRAM OF FLESH WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISE Y.

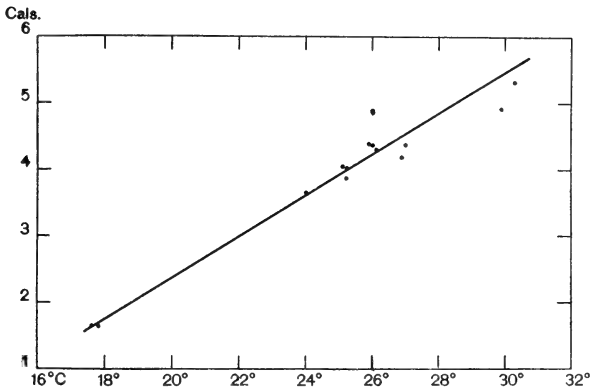


FIG. 93—STANDARD HEAT PRODUCTION PER KILOGRAM OF FLESH WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISE Z.

have to be curved upward for it to pass through the average of the points at the higher temperatures. This is contrary to the picture shown in the other charts for Y. It seems best therefore to allow the line to follow more nearly the general trend indicated by the majority of the observations, and in that case the line at 18° would start at a level considerably above the one value established at 18°, indeed a level nearly twice as

high as that found by actual measurement. Undoubtedly the heat production of the land tortoise at  $18^{\circ}$  is very small, because the temperature is too low to permit full physiological functioning. Usually tortoises are maintained at a much higher temperature and are in better condition at higher temperatures. The maximum standard heat production of Y per square meter of body surface was 91 calories at  $30^{\circ}$  C. Projection of the straight line as laid on figure 94 to  $37^{\circ}$  would indicate a probable metabolism at this temperature of approximately 110 calories. If the position of the line were changed so that it took more into consideration

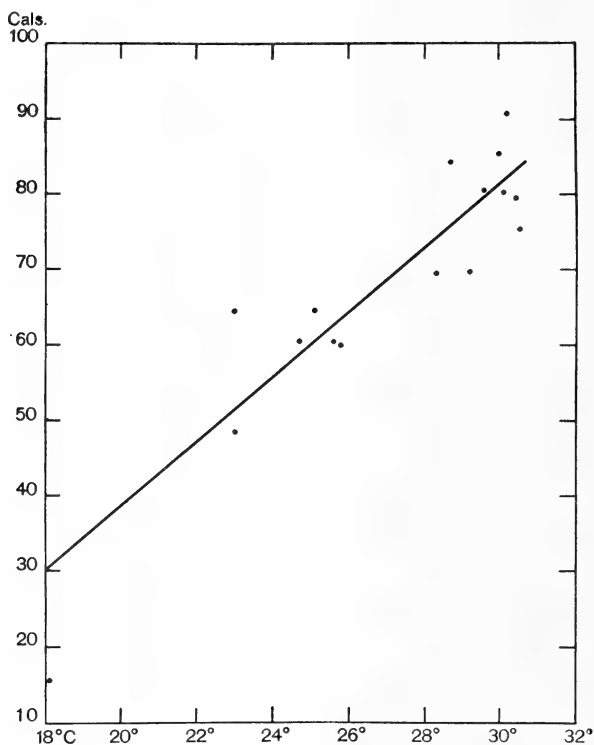


FIG. 94—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISE Y.

the one measured value at  $18^{\circ}$ , the projection of the line to  $37^{\circ}$  might then bring it to a level of 115 or 120 calories, but hardly more than that.

Since with Z two values were established at  $18^{\circ}$ , it seems justifiable to start the curve in chart 95 at the level shown by these two points. The increment in the general trend of the metabolism is then slightly different from that noted with Y. At  $30^{\circ}$  the line cuts the ordinates representing heat production at 76 calories, as compared with 82 calories with Y. Projection of the curve for Z to  $37^{\circ}$ , assuming a straight-line functioning of the temperature effect, would indicate slightly less than 110 calories per square meter of body surface.

The trend of the metabolism of both tortoises is characterized by being a straight-line function of the temperature. If these lines were projected to  $37^{\circ}$ , the heat production per square meter of body surface per 24 hours would be about 100 calories on the average. It is of interest likewise, in consideration of the fact that many observations have been made on cold-blooded animals at  $16^{\circ}$ , to note that if these lines were projected backwards to  $16^{\circ}$  they would indicate a probable heat production for Y of, at the maximum, 22 calories and for tortoise Z of 15 calories. If the line for Y were to be influenced by the single point at  $18^{\circ}$ , the metabolism at  $16^{\circ}$  might be somewhat under 10 calories. But since the two values for Z at  $18^{\circ}$  agree so well, it would seem as if they represent more accurately the true metabolism of the tortoise at this level, and that some extraneous factor entered into the measurement of Y at  $18^{\circ}$  C.

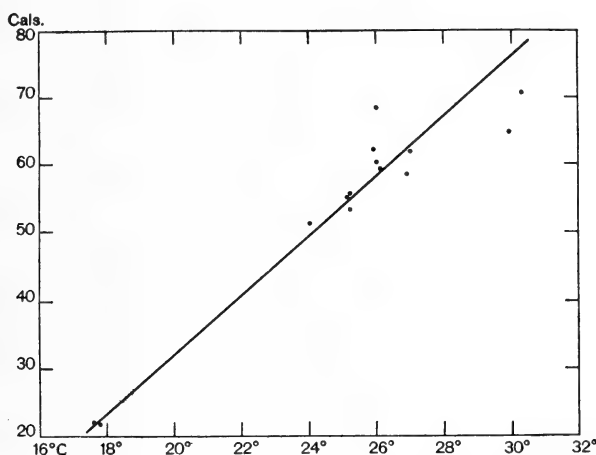


FIG. 95—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—TORTOISE Z.

#### INFLUENCE OF A SHORT PERIOD OF FASTING UPON STANDARD METABOLISM

With Y the standard metabolism was measured on two different occasions when it had been fasting for from 6 to 8 days and on one occasion when it had been fasting 10 days. Perhaps the simplest method of studying the influence of a short fast on the metabolism of this animal is to note the location of the various plotted points for the days of fasting, with reference to the curve on any one of the standard metabolism charts for this tortoise indicating the general trend of the metabolism. According to table 110 (p. 387) the heat production of Y per square meter of body surface per 24 hours on October 15, when it had been 10 days without food and was at a temperature of  $28.7^{\circ}$ , was 84.3 calories. Examination of the plotted data in figure 94 shows that the point corresponding to 84.3 calories at  $28.7^{\circ}$  is distinctly *above* the general curve. In other words, no evidence of a low metabolism is to be noted from the location of this point with reference to the general plotting on this chart. If the results for the longest fasting period in September are

considered, however, that is, on September 26 when the tortoise had been fasting 7 days at a temperature of  $18.1^{\circ}$ , it is seen that the heat value per unit of surface area, 15.5 calories, is not only the lowest point on the chart shown in figure 94 but is the aberrant point that has been touched upon several times in the discussion thus far.

Tortoise Z fasted twice during September, during a period of 8 days (September 19) and again (September 30) during a period of 7 days (table 111, p. 388). The heat production per square meter of body surface per 24 hours on September 19, when the temperature was  $25.1^{\circ}$ , was 55 calories. This value lies almost exactly upon the straight-line curve drawn through the plotted data in figure 95 (p. 393), and there is no indication of a distinctly low metabolism after 8 days of fasting. On September 30, after 7 days of fasting at a temperature of  $17.6^{\circ}$ , the metabolism is low, as is to be expected because of the low environmental temperature. It is not so low, however, as to suggest that the line laid through the plotted data in figure 95 should be curved rather than straight to represent the course of the metabolism with increasing temperatures.

*Fasting for from six to ten days* was apparently *without effect* upon the standard metabolism of Y and Z, either per kilogram of total body weight or of flesh weight or per square meter of body surface. Since, as is well known, the tortoise—not necessarily this particular type but certainly the Galapagos tortoise—has lived for months without food, this finding is perhaps not surprising. On the other hand, it is to be recalled that with the small Indian python a fast of about 150 days (not hours) resulted in a much lower level of metabolism than that obtaining after a fast of about 40 to 70 days. It is clear, therefore, that fasts of but five or six days are wholly without influence upon the metabolism of the tortoise. Time was not available to prolong the fasts of Y and Z to note whether the metabolism would finally be much lower, as was the case with the python after 150 days without food.

#### COMPARISON OF STANDARD METABOLISM OF TORTOISES IN SERIES OF 1915-1917 AND 1930

In the comparison of the heat production of the tortoises studied in this research it is especially to be reiterated that there were two weight groups. In one group the tortoises weighed approximately 5 kg. each (total weight). In the other group they weighed from 69 to 132 kg. With all but two of the tortoises the experiments were made at the New York Zoological Park between 1915 and 1917, with the best technique available at that time and under the skilful operation of a long trained member of the Nutrition Laboratory staff, Mr. Edward L. Fox. A second series of experiments was made with two tortoises in 1930 at the Nutrition Laboratory in Boston by Mr. Fox, but with a more highly perfected technique, perfected with the special view of obtaining information with regard to the respiratory quotient. Thus these observations extended over a period of fifteen years. The standard metabolism of each tortoise with reference to environmental temperature has already been discussed in the foregoing pages. The comparison of the metabolism of the tortoises as a whole will be made upon

the same bases as were employed in analyzing the data for each individual animal, with again due cognizance of the problems presented by the inactive shell and the estimation of the flesh weight and the surface area. So far as the 5-kg. tortoises are concerned, the potential errors in such calculations play practically little rôle in any of the methods of presentation, for these animals at the start were essentially of the same size. The greatest difficulties are encountered in attempting to compare the giant tortoises with the 5-kg. tortoises.

In the comparison of the metabolism of all the tortoises per kilogram of total body weight, two different factors must be taken into consideration, one the profound influence of temperature and the other the influence of size. The factors of age and sex can not be considered, for nothing is known

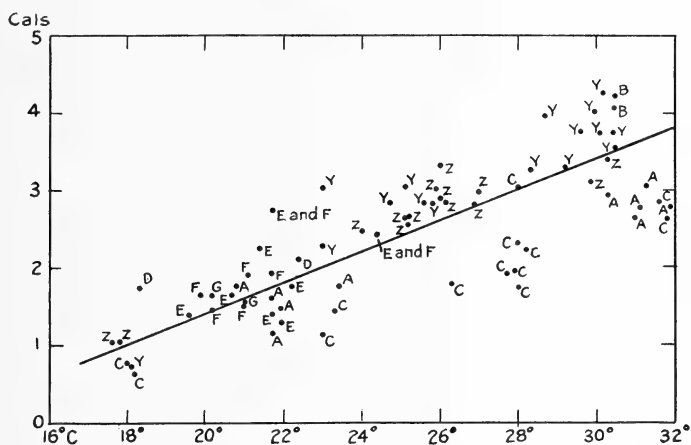


FIG. 96—STANDARD HEAT PRODUCTION PER KILOGRAM OF TOTAL BODY WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—ALL TORTOISES.

Tortoises A to D, inclusive, and Y and Z weighed about 5 kg. each. Giant tortoises are represented by animals E, F and G.

regarding the age and the sex of these animals. The concavity of the tortoise plastron is usually taken as an index of the male sex, but certainly in the case of Z, although the plastron was definitely concave, several eggs were found in the body. With both Y and Z and with the tortoises of the 1915-1917 series the curves indicating the general trend of the metabolism were found to be straight-line curves, altogether different from the curves obtained with the snakes and the lizards. Consequently one is quite prepared to find that the plotted points for the standard heat production per kilogram of total body weight for all the tortoises (fig. 96) as referred to the environmental temperature do group for the most part about an essentially straight-line curve. It is of special interest in this chart to note the different animals whose metabolism values deviate most widely from the central tendency. It is clear that C has a standard metabolism on the whole, over the entire temperature range, consistently lower than that of any of the other tortoises, since all but one of the plotted

points for C lie below the general curve. The same thing may be said for A. Above the curve are found the two values for B (determined at the same temperature) and the two values for D. The temperature range over which the larger tortoises were studied was more restricted than in the case of the 5-kg. animals. However, in spite of the narrow temperature range, the data obtained are fairly evenly distributed either side of the central tendency. One of the values for E and F, when studied together, that at  $21.7^{\circ}$ , is high and the other lies very close to the straight-line curve. The 1930 experiments with Y and Z show values above the curve for the

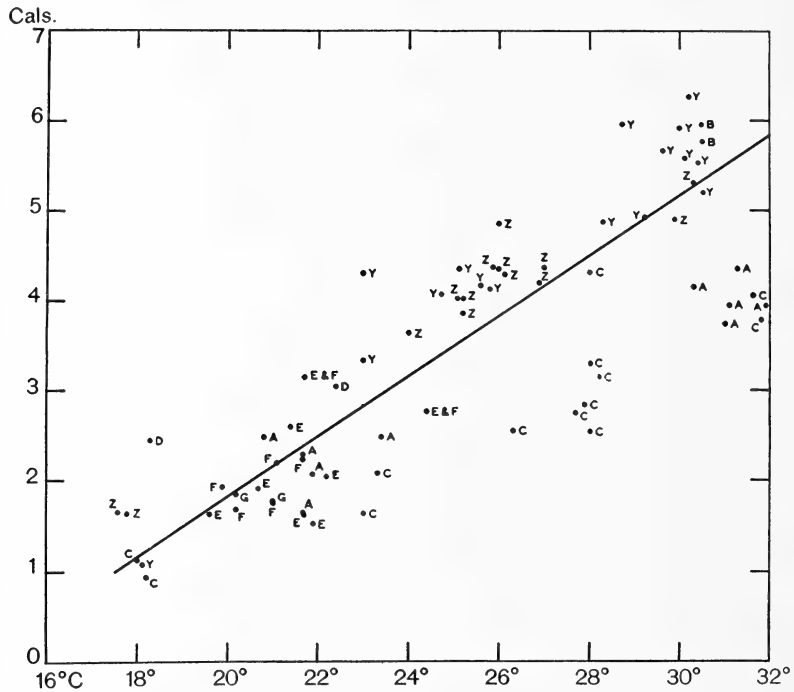


FIG. 97—STANDARD HEAT PRODUCTION PER KILOGRAM OF FLESH WEIGHT PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—ALL TORTOISES.

Tortoises A to D, inclusive, and Y and Z each weighed about 5 kg. (total weight). Giant tortoises are represented by animals E, F and G.

greater part of the entire temperature range. Of special interest are the values for the largest tortoise, G. This was measured at  $20.2^{\circ}$  and at  $21^{\circ}$ , and both values are near the line showing the central tendency. In general, therefore, it is justifiable to state that all these animals showed practically the same heat production *per kilogram of total body weight* at the different environmental temperatures and practically the same reaction to environmental temperature. In view of the difference in the probable weights of shell of these different sized tortoises, the shell of the 5-kg. animal representing approximately 30 per cent of the total weight and that of the 132-kg. tortoise about 15 per cent, this uniformity in the standard heat production per kilogram of total body weight is astonishing. The

standard heat production increased between 18° and 28°, as shown by the slope of the curve in figure 96, from 1.0 to 3.0 calories or 300 per cent.

Because of the general uniformity in the standard metabolism of all the tortoises per kilogram of *total* body weight and because the proportion of metabolically inert shell is considerably smaller with the larger than with the smaller tortoises, it is only natural to expect that when the heat production per unit of flesh weight is plotted with reference to the environmental temperature (fig. 97), the distribution of the plotted points will be much greater than on the basis of total body weight, and hence the picture will be somewhat different. A straight-line curve again probably represents the nearest approach to the general trend. In figure 97 all the values for C lie below the line, and at the temperature of 28° five out of six are considerably below the line. All but one of the values for A are below the line. One is slightly above it. All the values for B and D are above the line. The results for the larger tortoises, E, F and G, are again fairly well distributed on both sides of the curve, and of the two values for E and F, when studied together, one lies above and one below the line. The 1930 data for Y and Z lie for the most part above the line. It is clear that the calculation of the weight less shell has introduced a factor which results in a wider dispersion of the plotted heat values, and hence on this basis of reference it would be somewhat more difficult to predict the standard metabolism of a tortoise of known weight at the various temperatures. Even if the 5-kg. animals alone are considered, the percentage weight of shell of which is probably more correctly established than is that of the larger tortoises, the plots for the heat values per kilogram of flesh weight are more widely scattered than are those per kilogram of total body weight. In other words, if one were to consider these charts as offering at all a means of predicting the probable heat production of 5-kg. tortoises, the heat production per kilogram of body weight would be best approximated by reference to the *total* body weight.

In figure 98 the metabolism per unit of surface area has been plotted with reference to the environmental temperature. With animals of widely varying weights the heat production is supposed by the majority of writers to be more uniform per square meter of body surface than per kilogram of body weight. Hence the tremendous dispersion of the plotted values in figure 98 is surprising, to say the least. With a scatter as wide as here shown, the laying on of a curve of any type is questionable. The points deviating the most widely from the central tendency are those for the larger tortoises, E, F and G, and E and F when studied together. This scatter immediately challenges the method of computing the surface area, which includes, in the last analysis, the method of computing the weight of shell. If the discussion is confined exclusively to the 5-kg. tortoises, with which there were no large differences in weight, one would expect *a priori* to find no advantage in referring the metabolism to the surface area. In the formula  $S = K \times w^{2/3}$ , if K is constant and w remains constant (as it is essentially with these 5-kg. tortoises), the picture should be, and indeed is, much the same in the chart showing the metabolism per unit of surface area as it is in the two charts showing the



metabolism per unit of total body weight and per unit of flesh weight. The general distribution of the plotted points is much the same in all three cases. The striking feature in the comparison on the basis of body surface is therefore the wide dispersion of the values for the giant tortoises.

In laying a curve through the data plotted in figure 98, the values for the giant tortoises have been disregarded. For the 5-kg. animals a straight

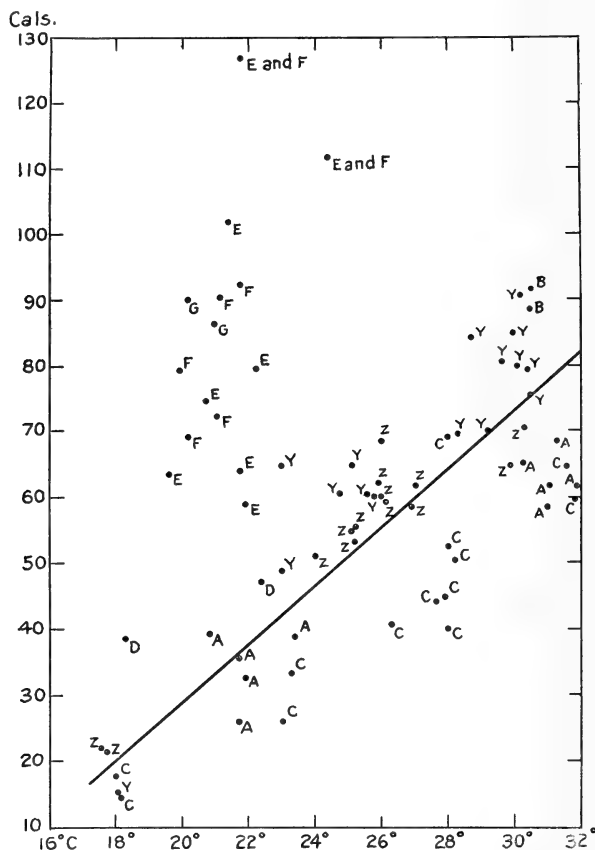


FIG. 98—STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS REFERRED TO ENVIRONMENTAL TEMPERATURE—ALL TORTOISES.

Tortoises A to D, inclusive, and Y and Z weighed about 5 kg. each. Giant tortoises represented by animals E, F and G. Straight-line curve indicates trend of metabolism only of 5-kg. animals.

line again represents the best indication of the general trend of the metabolism per square meter of body surface, and here again, as in the preceding charts, all but one of the values for A and C lie below the line and the majority of the values for Y and Z lie above the line. In other words, the picture is not greatly altered, except for the wide scatter of the points for the larger tortoises. The comparison of the metabolism of the giant tortoises with the metabolism of the smaller tortoises remains therefore

practically an unsettled problem. Although on the basis of flesh weight, the actual percentage of the inert shell may not have been as accurately calculated as one could wish and as should be determined by autopsies of tortoises dying in any zoological parks, nevertheless a gross error in this percentage calculation is probably not present. That being the case, it is difficult to understand why the metabolism of the different tortoises per unit of total body weight should be relatively more uniform than that per unit of flesh weight. It is certainly true that the two comparisons on the basis of the body weight less weight of shell and the body surface do not give anywhere near as uniform a picture of the metabolism of tortoises of widely varying weights as is shown by the comparison of the heat production per kilogram of total body weight. According to this latter comparison, it would seem as if at any given temperature the standard heat production per kilogram of *total body weight* of a tortoise weighing 132 kg. was the same as that of one weighing 5 kg.

#### RESULTS BY OTHER INVESTIGATORS ON RESPIRATORY METABOLISM OF THE TORTOISE

The study of the respiratory metabolism of the tortoise that has interested us most keenly in connection with our work is that of Rubner.<sup>1</sup> The details of his measurements on the tortoise appear on many pages of this monograph and are cited in many of the tables. Aside from Rubner's measurements, but few observations on the respiratory metabolism of the tortoise have been reported in the literature. In 1891 Chapman and Brubaker<sup>2</sup> made an experiment of 96 hours on a turtle weighing 1.7 kg. The authors state that their apparatus was not well adapted to the study of the lower vertebrata and that they report this measurement simply to show how slowly oxygen is consumed by such an animal.

A number of observations were reported by Buytendijk<sup>3</sup> in 1910 on tortoises and turtles varying in weight from 71 to 1650 grams. The environmental temperature was from 19° to 20°, except for one measurement at 23°. The heat production, which we have calculated from the measured carbon-dioxide production at an assumed respiratory quotient of 0.76, varied from 3.9 to 47.2 calories per kilogram of computed flesh weight (two-thirds of total weight) per 24 hours, with an average well above 15 calories. On the body surface basis, it ranged from 36 to 188 calories, and averaged 114 calories. According to the smoothed curves in figures 97 and 98 (pp. 396 and 398), the standard heat production at 19° of the tortoises studied by the Nutrition Laboratory averaged 1.5 calories per kilogram of flesh weight and 24 calories per square meter of body surface or much lower than that of the animals studied by Buytendijk. The one instance when Buytendijk definitely records that the animal was restless has not been included in the above comparison, but it would appear as if the degree of repose of the other animals was not as great as Buytendijk thought. His animals weighed much less than ours, but it is hardly

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, pp. 280 *et seq.*

<sup>2</sup> Chapman, H. C., and A. P. Brubaker, *Proc. Acad. Nat. Sci., Phila.*, 1891, p. 13.

<sup>3</sup> Buytendijk, F. J. J., *Proc. Section of Sci., Royal Acad. Sci., Amsterdam*, 1910, **13**, p. 48; *ibid.*, *Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd.*, 1910, **18**, p. 870.

conceivable that the difference in size could account for the entire difference in the metabolism of the two groups.

Hall's measurements on turtles<sup>1</sup> show that the metabolism between 0° and 29° increases with the increase in temperature. The values for heat production (calculated by us from the oxygen consumption at an assumed caloric value of 4.7 calories per liter) per kilogram of flesh weight are 5.0 calories at 18°, 8.5 calories at 20°, 6.5 calories at 22°, 7.7 calories at 25°, and 8.8 calories at 29°. These values all lie appreciably above the smoothed curve shown in figure 97, indicating the general trend of the metabolism per unit of flesh weight of the tortoises studied by the Nutrition Laboratory. They are likewise higher than any of the individual points plotted in figure 97. Per square meter of body surface the values are 38, 82, 52, 54, 59 and 67 calories at temperatures of 18°, 20°, 20°, 22°, 25° and 29° C., respectively. On the square meter basis, the heat values for Hall's turtles are, with the exception of the value of 82 calories at 20°, within the range of the data found with our 5-kg. tortoises and plotted in figure 98.

With painted turtles, fasting four weeks, Baldwin<sup>2</sup> found that the oxygen consumption at 20° C. averaged 0.0261 c.c. per gram of weight per hour. The average weight was 1200 grams. We have calculated the 24-hour heat production (caloric value of a liter of oxygen assumed to be 4.7 calories and flesh weight two-thirds of total weight) as 4.4 calories per kilogram of flesh weight and 41 calories per square meter of body surface. Here again the value per kilogram of flesh weight is outside the range noted with our tortoises, but that per square meter of body surface, though above our smoothed curve in figure 98, agrees well with the value found with our tortoise A at about 21° C.

Although the respiratory quotients reported by Issekutz and Végh<sup>3</sup> for turtles seem incredibly high, we have assumed a quotient of 0.72 and computed the heat production from the carbon-dioxide production, the measurements of which are probably more nearly correct. Thus, if the flesh weight is assumed to be two-thirds of the total weight and the body surface is calculated from the two-thirds power of the flesh weight times 10, one finds that their three turtles under normal conditions (without insulin), at temperatures between 18° and 20°, produced, respectively, 2.9, 3.8 and 3.1 calories per kilogram of flesh weight per 24 hours and 26, 33 and 24 calories per square meter of body surface. The metabolism per unit of flesh weight is twice as high in comparison with that of our tortoises, which averaged 1.5 calories at 19° (fig. 97, p. 396). This may be explained by the difference in body weight, for the turtles of Issekutz and Végh weighed on the average only about 1 kg. (total weight) whereas all but three of ours weighed around 5 kg. On the surface-area basis the results agree extraordinarily well with our data, which average 24 calories at 19° C. (fig. 98, p. 398).

<sup>1</sup> Hall, F. G., *Journ. Metab. Research*, 1924, **6**, p. 393.

<sup>2</sup> Baldwin, F. M., *Amer. Journ. Physiol.*, 1926, **76**, p. 196.

<sup>3</sup> Issekutz, B. v., and F. Végh, *Biochem. Zeitschr.*, 1928, **192**, p. 383.

## METABOLISM OF THE TORTOISE DURING DIGESTION

The digestion experiments thus far considered in this report have been confined to the snake and have dealt with the effect upon metabolism of the ingestion of protein, the natural food of the snake, and the ingestion of beef fat forcibly fed. The disposition of Y and Z to eat bananas freely

TABLE 112—*Influence of digestion of carbohydrate on the metabolism of the tortoise*

Tortoise and date	Time without food	Environmental temperature	R. Q.	Calories per kg. (total weight) per 24 hrs. <sup>1</sup>	Maximum increase above baseline
1930	days hrs.	°C.			p. ct.
Tortoise Y:					
Oct. 4	3	30.1	1.35	7.13	
Oct. 6	1 0	29.4	1.13	5.93	
Oct. 7	1 20	30.2	.93	4.28	
Oct. 8	3 0	30.4	.81	3.74	98
Oct. 11	6 0	29.6	.85	3.79	
Oct. 13	8 1	29.2	.73	3.29	
Oct. 9-15	4-10	28.5	.78	3.63	
Oct. 29	<sup>2</sup>	28.5	1.22	9.18	153
Tortoise Z:					
Sept. 11	3	25.6	1.17	3.71	
Sept. 11	6	26.2	1.17	4.35	
Sept. 12	1 2	26.8	1.06	3.30	
Sept. 12	1 5	27.5	1.06	2.99	
Sept. 13	2 3	24.1	.96	2.47	
Sept. 15	4 3	25.4	.75	2.68	67
Sept. 16	5 2	26.1	.72	2.86	
Sept. 17	6 0	26.0	.75	2.90	
Sept. 18	7 1	25.2	.73	2.57	
Sept. 19	8 3	25.1	.74	2.66	
Sept. 29-30	6-7	17.7	.76	1.06	
Oct. 27	6	17.2	1.36	4.00	277

<sup>1</sup> Heat production computed from measured oxygen consumption at caloric value of determined respiratory quotient. When the quotient was between 1.00 and 1.10 the caloric value of oxygen was assumed to be the same as that at 1.00. When the quotient was above 1.10 the caloric value of a liter of oxygen was assumed to be 5.4 calories (as a result of unpublished experiments at the Nutrition Laboratory on geese).

<sup>2</sup> Ate on Oct. 29; time not known; probably 3 to 5 hours after food.

made it possible to carry out a few observations regarding the influence of digestive activity upon their metabolism at a low as well as at a high environmental temperature. The results of these digestion experiments, so far as the respiratory quotient is concerned, have already been reported in table 107 (p. 371). Details regarding two digestion experiments with Y and two experiments with Z, for which actually determined baseline values are available for comparison, are given in table 112. In these experiments the metabolism was not measured in continuous periods without interrup-

tion over a number of days, as in the case of the digestion experiments with the snakes, but only over an interval of from 2 to about 8 hours. The excess calories due to the ingestion of the carbohydrate can not therefore be computed, but at least the approximate peak to which the metabolism rose after food can be noted.

With Y a series of observations from October 4 to 13 are available. This animal ate 40 grams of banana on the morning of October 4 and 104 grams on the morning of October 5, and had been eating freely before this. The maximum heat production was noted on October 4, when it had been 3 hours without food, namely, 7.13 calories per kilogram of total body weight per 24 hours. On October 8, 11 and 13, that is, from 3 to 8 days after food, the heat production averaged 3.61 calories. This evidently represents the baseline value, for observations on September 23, 24 and 25, when the tortoise had been from about 4 to 6 days without food indicated that the standard heat production at essentially the same environmental temperature as during this digestion period ( $29.8^{\circ}$ ) averaged 3.77 calories. It is thus seen that on October 4 the tortoise's heat production was 98 per cent higher than it was from October 8 to 13, or, in other words, twice as great as the baseline value. The use of the average value of 3.61 calories for October 8, 11 and 13 as the baseline may be called in question, and one might argue that the baseline taken from the curve for Y in figure 90 (p. 389) would be better. As a matter of fact, this baseline would be 3.9 calories or not far from 3.61 calories, so that there would not be a great difference in the calculated percentage increment, whichever value were used.

A still more striking increase in metabolism was noted in the experiment of October 29 at  $28.5^{\circ}$ , a slightly lower temperature than in the experiment cited above. The heat production during two well-agreeing half-hour periods averaged 9.18 calories. About 3 to 5 hours before these observations, Y had eaten 161 grams of banana. Baseline values at the same environmental temperature,  $28.5^{\circ}$ , were obtained on October 9 and 15 and averaged 3.63 calories. According to the curve in figure 90, the standard heat production at  $28.5^{\circ}$  would be essentially this same value, and 3.63 calories has accordingly been accepted as representing the baseline. The increase in metabolism due to the ingestion of the banana was therefore 153 per cent, that is, the metabolism after food was two and one-half times the baseline.

With Z the influence upon its metabolism of the ingestion of banana was studied on a number of days between September 11 and 19, at an average environmental temperature of  $25.8^{\circ}$ . The amount of banana eaten is not known, but it is significant that the heat production rose to a maximum value of 4.35 calories per kilogram of total body weight per 24 hours, at the sixth hour after food. Here again one might argue that the best baseline for comparison would be that taken from the general curve for Z in figure 91 (p. 390). The values obtained on Z at  $26^{\circ}$  are so numerous that the curve shows a baseline at this temperature of 2.8 calories or nearly the same as the average of the two actually determined values on September 18 and 19, *i.e.*, 2.61 calories. If the average of 2.61 calories is

accepted as representing the baseline, it can be seen that the maximum heat production 6 hours after food was more than one and one-half times the baseline, that is, there was an increment of 67 per cent.

Another digestion experiment was made with Z on October 27 at a low environmental temperature averaging 17.2° C. On September 29 and 30 the animal was found to have a standard heat production at 17.7° averaging 1.06 calories. According to the curve for Z in figure 91 the standard heat production at 17.2° would be 0.88 calorie, but the actually measured value of 1.06 calories will be used for the comparison. One month later, about 6 hours after Z had eaten 185 grams of banana, the heat production was found to be 4.00 calories. This observation was obtained during three consecutive periods totaling two hours. Immediately preceding these three periods, the animals had been subjected within 83 minutes to a transition in environmental temperature from about 29° to 14.8° C. It may be that its metabolism in these 83 minutes had not reached the true level characteristic of the lower temperature, although its body temperature (as will be seen from page 349) was probably not far from 17° or 18° C. On the assumption that the value of 4.00 calories does represent the effect of an environmental temperature of 17.2°, it is computed that the metabolism at this temperature level and 6 hours after food was four times as great as the standard metabolism, that is, there was an increment of 277 per cent.

The chief significance of these digestion experiments is that they bring out the fact that by the ingestion of a protein-poor but carbohydrate-rich meal (banana) the metabolism of the cold-blooded tortoise may be increased from two to three times. According to the tables of Atwater and Bryant<sup>1</sup> the edible portion of the banana has a fuel value of 460 calories per pound, that is, about one calorie per gram. The protein content is 1.3 per cent. This would correspond to 0.2 per cent nitrogen. The standard energy requirements of Y between 28° and 30° have been estimated to be not far from 3 or 4 calories per kilogram of total body weight per 24 hours, or roughly speaking, 15 total calories per day. Hence the ingestion of 110 grams of banana would correspond to the total "standard" fuel needs for approximately 8 days. Since on the first day or two after food ingestion the tortoise certainly has a very greatly increased metabolism, an increase which may amount sometimes to as much as 100 per cent or over, the energy needs for the first one or two days might be 30 instead of 15 calories, thus reducing the number of days during which the fuel material would meet the tortoise's needs. Apparently with both Y and Z the peak of digestion had passed after about 50 hours. On October 27 when Z had eaten 185 grams of banana or practically 185 calories, the total standard energy needs amounted to about 5 total calories, since the tortoise weighed 4.3 kg. on this date. Hence 185 calories would cover its energy needs under standard conditions for about 35 days. But as the actual heat production 6 hours after food was 4 calories per kilogram of total body weight, that is, 17 instead of 5 total calories per day, the number of days during which the 185 grams of banana would meet the energy needs of the

<sup>1</sup>Atwater, W. O., and A. P. Bryant, U. S. Dept. Agric., Office Expt. Sta., Bull. 28, 1906, p. 71.

animal would be reduced somewhat. A conservative estimate would be that the 185 grams of banana would represent the standard energy needs at this low temperature for a period of from 25 to 30 days.

This finding with the tortoise is similar to that noted with the steer,<sup>1</sup> that is, that an essentially pure carbohydrate diet results in a great increase in the metabolism. The significant feature of the digestion experiments with the tortoise is that this stimulus obtains even at a low temperature of 17° C., when the metabolism is at an extremely low level. In the discussion of the respiratory quotients of these tortoises, emphasis was laid upon the capacity of these cold-blooded animals, with their sluggish metabolism, to transform large quantities of carbohydrate into fat, as shown by the high respiratory quotients. To this conclusion may be added a further fact, namely, that the ingestion of a carbohydrate-rich, protein-poor food results in an enormous increase in the standard metabolism of the tortoise.

### GENERAL CONSIDERATIONS ON METABOLISM OF LARGE COLD-BLOODED ANIMALS OF DIFFERENT SPECIES

The experimental evidence presented in this report should be examined not only for itself alone but, in so far as possible, with reference to the findings on cold-blooded animals in earlier researches. In the Nutrition Laboratory's investigations on cold-blooded animals, as previously stated, only the larger animals were studied, for our object was to add to the knowledge of comparative physiology in the hope of further elucidating, ultimately, some of the perplexing problems in human physiology. It was obvious that, particularly in dealing with energy transformations, the more closely the cold-blooded animals used approached the size of humans or of other commonly studied warm-blooded animals, the more logical would be any comparisons of the metabolism of these two main groups of animals. Consequently the comparison of our results with the findings of other investigators will emphasize the few reports in the literature dealing with metabolism measurements upon the larger cold-blooded animals.

Too little is known regarding the general physiology of cold-blooded animals. Hence any carefully recorded observations of whatever nature are of importance at this stage of knowledge on this subject. For this reason a considerable number of incidental observations have been reported in the foregoing pages, regarding such factors as the rectal and the skin temperature, the heart rate, the respiration rate and the insensible perspiration. But the main thesis of the Nutrition Laboratory in its research on cold-blooded animals was a study of the respiratory metabolism, since a comparison of the metabolism of cold-blooded with that of warm-blooded animals, specifically man, was particularly desired. Therefore in the following comparison of large cold-blooded animals of different species

<sup>1</sup> Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 377, 1927, pp. 223 *et seq.*

among themselves, preliminary to a comparison of warm-blooded with cold-blooded animals, the heat production will be considered primarily, with some discussion of the relationship between the water of vaporization and the heat loss.

#### FACTORS TO BE CONSIDERED IN ACCUMULATING COMPARABLE METABOLISM MEASUREMENTS ON COLD-BLOODED ANIMALS

With cold-blooded as well as with warm-blooded animals, metabolism measurements are comparable only when the effects of activity, digestion and changes in environmental temperature are ruled out. According to ocular observations the cold-blooded animal, particularly the snake, usually remains remarkably quiet during the period of experimentation, certainly much quieter than do any of the warm-blooded animals. It is believed that the general sluggishness of the cold-blooded animals has led to a false impression concerning the amount of muscular activity that they engage in, and particularly concerning the effect of this activity upon their metabolism. The movements of the snake are usually slow and deliberate and do not last any great proportion of the experimental period, but almost invariably such movements, slow and small though they may seem, are accompanied by a definite increase in metabolism with, at times, a fairly pronounced change in the ratio between the carbon-dioxide production and the oxygen consumption, a change greater proportionately than would be expected from the relatively small amount of movement occurring. Indeed, muscular activity of any degree on the part of the snake and probably of the tortoise, although apparently slight when compared with the commonly encountered respiration chamber activity of warm-blooded animals, will play a relatively large rôle in the metabolism. All writers on metabolism have recourse to the belief that suspected, although often unproved, variations in the degree of repose may explain any variations noted in the metabolism. It is therefore imperative in all metabolism experiments made for comparative purposes, either with warm-blooded or with cold-blooded animals, that graphic records of the degree of repose or degree of activity should be obtained. Such records make it possible to rule out immediately, as not basal or standard, experimental periods that otherwise would be assumed to have been obtained during periods of complete repose.

Digestive activity, unless one is studying primarily the digestive processes, should likewise be avoided in comparative studies with cold-blooded animals. With these animals digestive activity persists for a much longer time than it does with warm-blooded animals, depending entirely upon the temperature of the environment and the temperature of the animal itself. The feeding habits of snakes and tortoises are such that one meal may have a relatively large caloric value, and the elaboration of this food into body material to be stored or burned requires a much longer time than 12 or 24 hours. This sustained reaction to the digestion of food at low temperatures is a factor that should not be disregarded. Rubner has frequently emphasized the importance of equality of nutritive condition, when comparing animals not only of the same but particularly of different



species. In the presentation of our data given in the foregoing pages we have attempted to indicate, in so far as possible, the nutritive condition of our cold-blooded animals, the time when last fed, and the kind and amount of food. But it is recognized that with these animals the factors of state of nutrition and stage of digestion present great uncertainties. It is possible, however, to rule out the influence of digestive activity with the cold-blooded animal, and it is especially worthy of note that the animal, having once reached the post-absorptive state, can be maintained at this level for a much longer time than can the warm-blooded animal without introducing the specific effect of undernutrition or fasting.

The most important factor to be taken into consideration in the comparison of cold-blooded animals is the pronounced influence of changes in environmental temperature, which is practically the temperature of the body itself in striking contrast to the situation with warm-blooded animals, whose body temperature may remain (as in the case of the polar fox)  $60^{\circ}$  C. or more above the environment. This temperature effect on the cold-blooded animal can hardly be overestimated. With the slightest change in the temperature of the cells, the metabolism is altered. Indeed, the rate of alteration is so generally uniform that it can almost be predicted. The fact that the measurement of the cell or rectal temperature is essential for the best series of comparisons rules out many of the investigations on the small cold-blooded animals, with which such temperatures can be determined only with difficulty. This makes it all the more advantageous to work with larger animals. Fortunately with many of our snakes and with two of the 5-kg. tortoises, it was possible to determine either the mouth or the rectal temperature frequently, so that a clear picture has been obtained of the relation between body and environmental temperature. The change in the heat production of the cold-blooded animal with each degree change in environmental temperature is of a much higher order than that of the warm-blooded animal, being often 20 per cent or more as compared with the maximum of 5 per cent with a few warm-blooded animals. It is therefore necessary, in comparing the metabolism of cold-blooded animals of different species, not only to discard any measurements affected by activity or digestion but particularly to bear in mind the influence of environmental temperature. In many of our measurements on the snake and other reptiles, precautions were taken to have the environmental temperature always the same. In many others, extremes in environmental temperature were purposely introduced, in order to secure information regarding the reaction of the metabolism of the cold-blooded protoplasm at different temperature levels. But in any comparisons of the metabolism of these animals the chief point to be noted is not whether the animals were quiet and in the post-absorptive state (these conditions definitely existed in our so-called "standard metabolism measurements") but what was the environmental temperature or, better still, the rectal temperature of the animals at the time the observations were made.

With the cold-blooded exactly as with the warm-blooded animal there is also the problem of how to compare individuals of different sizes, and all the complexities present in the attempt to equalize differences in size

of warm-blooded animals by referring the heat production to a common unit of body weight or body surface or to the two-thirds power of the body weight are present in the comparison of cold-blooded animals of different sizes.

Metabolism studies with cold-blooded animals present an unusual interest over studies with warm-blooded animals on account of the rôle played by the water vapor in the heat loss. With warm-blooded animals under conditions of repose and moderate activity, approximately 25 per cent of the total heat loss takes place in the form of water vapor and 75 per cent by radiation and partly by conduction.<sup>1</sup> With the cold-blooded animals there is probably not only no loss of heat by radiation and conduction but frequently an actual absorption of heat from the environment, and all the heat produced by the animal as well as the heat absorbed from the environment is given up by the vaporization of water. Hence metabolism observations on cold-blooded animals must not be confined, as is the case with warm-blooded animals, to measurements of the gaseous metabolism alone, but must include and emphasize a study of the water balance or water loss. Such observations, fortunately, we were able to make on two tortoises and a python. Precisely the same factors that influence the total metabolism, the oxygen consumption, and the carbon-dioxide production, likewise influence the water of vaporization in a large degree, and hence in any consideration of the water of vaporization one must take into account digestion, muscular activity, and particularly the environmental temperature.

No studies of the gaseous metabolism, the heat exchange, or the water of vaporization can in the case of cold-blooded animals be intelligently interpreted without a knowledge of the environmental temperature or, better still, the cell temperature at the time of measurement. In the tabular presentation of data obtained on our various groups of animals these factors have been taken into consideration. It now remains for us to compare all the cold-blooded animals that we have studied with special reference to the respiratory quotient, the total heat output and, in so far as possible, the water of vaporization. Fortunately the water of vaporization, which is difficult to determine directly, can be closely approximated by the measurement of the insensible perspiration, particularly since feces and urine are not voided frequently by these cold-blooded animals when fasting.

### CHARACTER OF KATABOLISM OF COLD-BLOODED ANIMALS

No other index of the level of vital activity compares for a moment with the measurement of the gaseous metabolism. To be sure, the heart rate reflects in a general way the vital activity, but it is by no means as sharp or true an index as is the gaseous metabolism. All earlier researches on cold-blooded animals have demonstrated that the gaseous metabolism responds immediately to changes in the temperature of the environment, showing that this index is an especially sensitive one. In any com-

<sup>1</sup> Soderstrom, G. F., and E. F. Du Bois. *Arch. Intern. Med.*, 1917, **19**, p. 931.

parison of the gaseous metabolism of the different species of cold-blooded animals one should consider not only the total metabolism or the total heat production, but also, since it is of equal importance to physiology, the *character* of the material katabolized both during complete fasting and during feeding.

#### CHARACTER OF KATABOLISM DURING FASTING

Among the cold-blooded animals such as we studied, the feeding habits vary greatly. The snake and the alligator eat animal food. The tortoise has a vegetarian diet. But during fasting, as has already been found to be the case with warm-blooded animals such as the carnivorous dog and the herbivorous steer, the metabolism of the cold-blooded animal tends to become uniform after a few days, and the animal thereafter subsists in large part upon stored fat. The rapidity with which the metabolism reaches a constant level naturally depends to a great degree upon the composition of the body, primarily upon the storage of preformed carbohydrates and secondly upon the storage of fat. Pecuniary reasons prevented us from killing our large cold-blooded animals and analyzing the body content, save in two instances. The actual composition of the body of these animals can therefore only be inferred from the state of nutrition, the food habits, and certain features of the study of the respiratory quotient, such as the rapidity of the assumption of a high quotient after carbohydrate feeding and the rate of fall from a high quotient to a fat quotient with the withdrawal of food. It is therefore upon this type of evidence that conclusions must be drawn as to the probable chemical composition of the body of the cold-blooded animal, with special reference to the carbohydrate storage. With regard to the storage of fat, it is well known that practically all cold-blooded animals are liberally supplied with fat reservoirs, which they usually keep fairly well filled. Only by virtue of this fact can they subsist the almost incredible length of time that has been noted in many cases. Here again analyses are, unfortunately, lacking. It is a fact, however, that tortoises are notably rich in fat. One of the main reasons for their near extermination on the Galapagos and other islands has been that the natives killed them and tried out the oil or fat. Most of the snakes with liberal feeding have every appearance of having large fat reservoirs, but here again there is no direct evidence. During complete fasting, however, our data show that the katabolism of these animals more or less quickly becomes that of pure fat. No matter at what nutritive level the fast is begun, whether at the high carbohydrate level of the liberally fed tortoise (which has a respiratory quotient as high as 1.3 or 1.4 when on full feed) or at the fat-protein level of the snake, a respiratory quotient characteristic of the combustion of fat usually appears after a short time. In this particular respect, certainly all our cold-blooded animals showed the same tendency, that is, a predominantly fat combustion after fasting.

The length of time after food when this predominantly fat combustion begins is not the same with the cold-blooded as with the warm-blooded animal. Thus with the rat, subsisting in large part upon a carbohydrate diet, and with the pigeon and the dove, subsisting exclusively upon a

carbohydrate diet, the fat quotient appears usually within 24 hours. With man the fat quotient is obtained only after the third, fourth, or fifth day of fasting. With the herbivorous warm-blooded animal the appearance of a fat quotient is still longer delayed, but even with the steer an essentially fat quotient usually is found by the end of the third or the fourth day. On the other hand, with the cold-blooded animal whose metabolism is at a very low level and whose capacity for eating is very large, as witnessed by the fact that the snake can eat enough food in one meal to supply its entire energy demands for several weeks, the length of time for the animal to reach the complete fasting stage after the withdrawal of food must be measured not in hours or days but in weeks. In other words, the fasting or fat quotient may not appear so rapidly with the fasting cold-blooded animal as with the fasting warm-blooded animal. The relatively large amount of protein mixed with fat in the snake's diet, which is chiefly animal food, does produce a somewhat higher respiratory quotient than the fasting quotient, but the fasting quotient is ultimately reached. The large amounts of carbohydrate ingested by the tortoise, on the other hand, are almost immediately transformed, in large part at least, into fat and deposited in the body. Since the supply of carbohydrates is fairly liberal, the respiratory quotient of the tortoise may be at a high level for some time, and the appearance of the fasting quotient is therefore a matter of days rather than hours, as in the case of the rat.

With prolonged fasting of the cold-blooded animal, a rise in the respiratory quotient to the level characteristic of protein combustion might be expected, corresponding to the pre-mortal rise in protein metabolism found with warm-blooded animals. It is by no means sure, however, that there would be such a rise. The length of time taken by the cold-blooded animal to reach the complete fasting stage and the very low metabolism make such a sharp differentiation in the character of the katabolism practically impossible. In many instances we do find, however, a respiratory quotient so considerably above that representing the combustion of fat as to lead us to believe that the animal was definitely burning rather considerable amounts of protein. This was particularly true with the snake and, to a certain extent, with the tortoise, so it is probable that a protein respiratory quotient might be found with prolonged fasting with either the snake or the tortoise. One wonders immediately what, for example, would be the respiratory quotient of a tortoise that had been without food for one year (as were those frequently taken on sailing vessels from the Galapagos Islands<sup>1</sup>) and what was the respiratory quotient of the large python at the New York Zoological Park that lived over 20 months without food. Unfortunately the answers to such questions can not even be conjectured.

#### RESPIRATORY QUOTIENTS BELOW 0.70

One feature of our study of the respiratory quotients of cold-blooded animals that is certainly worthy of more intense investigation and that may lead to the solution of some most important problems in intermediary metabolism is the finding of quotients definitely below 0.70. The experience of the Nutrition Laboratory in studies in comparative physiology,

<sup>1</sup> Van Denburgh, J., *Proc. Calif. Acad. Sci.*, 1914, 4th ser., 2 (I), p. 216.

dealing before this present research exclusively with warm-blooded animals, has been such that respiratory quotients below 0.70 have invariably been attributed to technical errors. We have not been willing to assume that these chance findings were anything more than accidents. It has not been possible always to state definitely where the error was, but the difficulty of duplicating the low quotient and the general absence of such low quotients have led us to look askance at such results. In this same frame of mind we began the observations upon the tortoise and the python in the fall and winter of 1930 and 1931. It soon became clear that under certain conditions respiratory quotients considerably below 0.70 not only were to be found but were to be found regularly in consecutive periods on the same day and, what is more important, under conditions that could be duplicated and the same values again recorded. The first instances of quotients of cold-blooded animals below 0.70 noted by us were with the tortoise in the fall of 1930, when a technique was available that permitted accurate determinations of the respiratory quotient. These instances have already been mentioned (see page 370).

Perhaps one of the most important features of our investigation in 1931 with the python was the establishment beyond doubt of the precise respiratory quotients obtaining under different conditions of temperature, feeding and activity. Judging from our experience with warm-blooded animals and to a certain extent with the fasting tortoise, we would expect that with a cold-blooded animal, such as the snake, the respiratory quotient during fasting would be not far from that of fat, although there might be a considerable protein katabolism. The respiratory quotient was determined in every metabolism experiment with the 1931 python, and not simply in one period but in several periods, sometimes six or seven on each day. The period values have been recorded in table 55 (p. 208) and it can be seen that, although occasionally an aberrant quotient appears, in general the picture is fairly clear and in some instances at least astonishing. The average quotients for the days when the so-called "standard metabolism" was measured, that is, the quotients presumably unaffected by digestive activity, have been given in table 56 (p. 211) and the average quotients for the days during the period of digestion in table 84 (p. 296). In table 56 it will be noted that the time since the snake was fed varied from 8 days in the first experiment on January 14 to 33 days in the last experiment. For a warm-blooded animal 8 days would be a long fast, but in view of the nature and the low level of the metabolism of the cold-blooded animal a fast of 8 days is but a mere incident in the life of many of these animals. The larger snakes would not normally feed oftener than once in two weeks or perhaps once a month, and evidences of very long periods of voluntary hunger have been recorded, so that 8 days can not be considered a long fast. One must really be guided by the length of time required for digestion, in determining whether the period of fasting has been a long one. In our digestion experiments with the boas it was shown that the length of time required for digestion is determined in large part by the temperature of the environment. It so happened, however, that in the experiment of January 14 with the 1931 python the highest average respiratory quotient of the entire series was

found, namely, 0.78. This is so measurably above the fat quotient that one can logically assume that there was a not inconsiderable amount of protein katabolism resulting from the ingestion of the guinea-pig 8 days before. The environmental temperature at the time this quotient was obtained was 26° C.

The quotients obtained after January 14 show considerable irregularity. Based upon our experience with warm-blooded animals, we would not assign any great physiological or biological significance to quotients that are below 0.68. But there are in table 56, too frequently to be disregarded, quotients approximating 0.60 or a little below, notably on January 19 and 20 and February 9, 10, 12 and 26. Our first finding of these low quotients on January 19 was most perplexing and called to mind the fact that in the 1930 tortoise series there was one day when the respiratory quotient in two experimental periods averaged 0.60. It began to appear as if this low quotient was a fact and a frequently occurring situation with our cold-blooded animals. The repetition of these low quotients with the 1931 python on so many subsequent days left the fact indisputable. A closer analysis of these particular experiments shows that on the days when very low quotients were found, the environmental temperature was usually below 20°. Indeed, the picture of quotients approximating 0.60 at temperatures of 18° or thereabouts was so clear that it could be definitely predicted that, by placing the snake at a temperature of 18°, its respiratory quotient, which the day before had been essentially that of fat, would fall to 0.60. This finding that the low environmental temperature occasioned low respiratory quotients was furthermore strikingly demonstrated by the experiments on February 9, 10 and 12, which showed that the quotient remained at a level of 0.60, not only for one day but for several days. As a matter of fact, the python had been maintained at a temperature of 20° or somewhat below ever since 10 p.m. on February 6, so there is evidence of the probable existence of a quotient of about 0.61 for six consecutive days. There was thus a definite level in the respiratory quotient, abnormally low though it seemed. Another striking fact is that, although the respiratory quotient on February 24 (when the rectal temperature was 38°) averaged 0.74, it was possible within forty-eight hours to produce a condition in which the quotient averaged 0.57 for three consecutive periods (table 55, p. 210). This was a real, permanent situation and there was no error in the experimental technique.

The explanation of this low quotient is not at hand. It was thought at first at the time of some of our earlier findings that there was, perhaps, a retention of carbon dioxide<sup>1</sup> by the snake, that is, that in the sudden subjection of the animal to cold the body fluids became saturated with

<sup>1</sup>The suggestion of Lusk (*Science of Nutrition*, 4th ed., 1928, page 121) that the tissues of an awakening marmot may hold less carbon dioxide at 37° than at lower temperatures is without doubt correct. Calculation, however, of the amount of carbon dioxide that could be retained by a cold-blooded animal when at a low temperature and subsequently released when at a higher temperature fails to account for any considerable part of the carbon dioxide that would have to be retained in order to be wholly or in large part responsible for the low quotients noted. Hall (*Journ. Metab. Research*, 1924, 6, p. 399) states that carbon dioxide may be stored in the tissues and the blood for some time or may be washed out of the lungs by ventilation in excess of the production. He concludes that "perhaps this is the explanation of the constantly decreasing respiratory quotient with decreasing temperatures."

carbon dioxide and that, because of the extremely low metabolism of the cold-blooded animal, a very large amount of carbon dioxide would not have to be retained to produce this lowering of the quotient. A partial support of this theory was found in a series of experiments made during the first two weeks of February. On February 7, after a number of respiration experiments at about  $31^{\circ}$  C., the environmental temperature was lowered to  $20^{\circ}$  and the insensible perspiration was determined in periods extending over two days. On February 9, 10 and 12 respiration experiments, each consisting of three consecutive periods, were made at  $18^{\circ}$  in which the respiratory quotient was found to be consistently between 0.60 and 0.63. On February 13 (table 55) the respiratory quotient was first established at a low temperature of  $18^{\circ}$ , and during the first two periods of the respiration experiment it was 0.58 and 0.60, that is, practically the same as on the day before and for two days before that.<sup>1</sup> The respiration chamber was then rapidly warmed so that in the third period the chamber temperature averaged about  $30^{\circ}$  C. It was maintained at close to  $30^{\circ}$  throughout the rest of the experiment. The respiratory quotient began to rise immediately, increasing from 0.60 to 0.65, 0.79 and 0.84 and then decreasing to 0.76, 0.64, 0.74, 0.80, 0.70, 0.65 and 0.71. The python was all this time at  $30^{\circ}$ . Although there is considerable irregularity in the last five or six quotients, they average not far from that of fat. It thus appears as if the python at  $18^{\circ}$  had a constant respiratory quotient of about 0.60, but that at  $30^{\circ}$  it had a fat quotient. There was evidence of the escape of a certain amount of absorbed carbon dioxide in that the respiratory quotient actually rose to as high as 0.84 in one of the periods.

According to the experiments of February 10 and 12 this snake at  $18^{\circ}$  gave off on the average 96 c.c. of carbon dioxide per kilogram of body weight per 24 hours and absorbed 156 c.c. of oxygen. The average respiratory quotient was thus 0.62. With a consumption of oxygen of 156 c.c. per kilogram of body weight per 24 hours, if the respiratory quotient were 0.71 there would be a production of carbon dioxide of 111 c.c. per unit of weight per 24 hours. On this basis, if the low quotient of 0.61 is explained by retention of carbon dioxide, the animal would have had to retain the difference between 111 c.c. and 96 c.c., or 15 c.c. of carbon dioxide per kilogram of body weight per 24 hours. Since the animal weighed at this time approximately 6 kg., the total retention of carbon dioxide per day would have been 90 c.c. From February 7 to 12, inclusive, or for at least 6 days, the snake had been living at a temperature of  $20^{\circ}$  C. or somewhat below and probably had had a low respiratory quotient during all this time. Hence in 6 days it might have retained at least 540 c.c. of carbon dioxide.<sup>2</sup> If the low respiratory quotient is due to the retention of

<sup>1</sup> This finding of low respiratory quotients persisting for several days at a low environmental temperature suggests that the conception of Pütter (*Zeitschr. f. allg. Physiol.*, 1905, 5, p. 566) may obtain, namely, that the anoxybiotic metabolism is to be considered as the more general or "primitive" scheme of animal metabolism and the oxidative processes as the secondary.

<sup>2</sup> The carbon-dioxide production on February 9, when the temperature was also  $18^{\circ}$ , was 86 rather than 96 c.c. per kilogram of body weight per 24 hours. But in making the above calculation it has been assumed that the production was more nearly 96 than 86 c.c. If the calculation is based on the lower value, the total amount of carbon dioxide retained would have been 900 c.c.

carbon dioxide, there should be a release of this carbon dioxide when the temperature of the animal is raised to 30° or more. On February 13 the respiratory metabolism of the python was measured during 12 consecutive periods, the first two at 18° and the remaining at about 31° or 32°. In the first three periods respiratory quotients of 0.58, 0.60 and 0.65 were obtained. In periods 4, 5 and 6 high quotients of 0.79, 0.84 and 0.76 prevailed. In these particular periods the carbon-dioxide production per kilogram of body weight per 24 hours was 205, 360 and 298 c.c., respectively. The agreement of these results is not satisfactory, but it may be assumed for purposes of discussion that the higher value obtained, that is, 360 c.c. The highest oxygen value during these three periods is 430 c.c. per kilogram of body weight per 24 hours. To obtain a respiratory quotient of 0.70 with an oxygen consumption of 430 c.c. would call for an excretion of 301 c.c. of carbon dioxide. Actually 360 c.c. were excreted, that is, there was an excess of approximately 60 c.c. per kilogram of body weight per 24 hours or, for an animal weighing 6 kg., a total of 360 c.c. per day. But the excess carbon dioxide as shown by the high respiratory quotients appeared only during three hours of measurement, periods 4, 5 and 6 being each one hour long. Therefore the excess carbon dioxide produced during this time was only one-eighth of 360 c.c., or 45 c.c. Since to produce the low respiratory quotient of 0.62 or thereabouts for 6 days would call for a retention of at least 540 c.c. of carbon dioxide, the amount calculated as having been released is but a small fraction of the total amount that should have been blown off. Hence the theory of the retention of carbon dioxide does not hold.

Another possible explanation of these low quotients is that the snake can excrete enough nitrogen gas, as such, to affect the analysis and produce the low quotient. This is a suggestion born of reading the report of Mareš.<sup>1</sup> But Mareš was living in the atmosphere of Seegen<sup>2</sup> and his associates, who thought that nitrogen was given off. Since that time investigations, particularly those of Krogh<sup>3</sup> and Oppenheimer,<sup>4</sup> have proved conclusively that nitrogen is not given off.

Apparently the katabolism of the cold-blooded animal at these low temperatures is of an entirely different type from that of the warm-blooded animal. It may be that at the low temperatures the cold-blooded animal is undergoing what would be, from the standpoint of the metabolism of the warm-blooded animal, considered as a perturbed metabolism. Possibly there is an absorption of oxygen, unaccompanied by the liberation of carbon dioxide. This would mean a formation of intermediary products in metabolism. But what products could be formed to give such low respiratory quotients is not known. Pages of speculation and of various hypothetical calculations could be written. That these intermediary products would not ultimately appear in the urine or feces, if passed, is highly

<sup>1</sup> Mareš, F., Bohemian Archives of Medicine, Journ. Advancement Med. Sci., Prague, 1889, 2, pp. 458-527. (English translation on file in the Nutrition Laboratory.)

<sup>2</sup> Seegen, J., and J. Nowak, Arch. f. d. ges. Physiol., 1879, 19, p. 347.

<sup>3</sup> Krogh, A., Skand. Arch. f. Physiol., 1906, 18, p. 364.

<sup>4</sup> Oppenheimer, C., Biochem. Zeitschr., 1906, 1, p. 177; *ibid.*, Biochem. Zeitschr., 1907, 4, p. 328; *ibid.*, Biochem. Zeitschr., 1909, 16, p. 45.



improbable. It is clear, at least, that the problem will never be solved until there is a more extended, complete analysis of the urinary and fecal excretions. These excretions will be small and infrequent at the low temperatures, so that from the standpoint of the mere collection of material the solution of this problem may not be expected for a considerable time. Unfortunately, it will be impracticable for the Nutrition Laboratory to carry the study any further. It is believed, however, that it has been definitely established that the character of the snake's katabolism may be such as to produce a constant respiratory quotient of 0.60 for a week at least. It is desirable to study the respiratory quotient of the snake during the transitional periods from a high to a low temperature and *vice versa*, to see if the quotient would always be higher at the high temperatures and lower at the low temperatures.

With warm-blooded animals a common interpretation of the low respiratory quotients occasionally found (although too frequently found with technique that may be challenged) has been the supposed transformation of fat into carbohydrate, a long-debated point. With such little knowledge regarding the normal glycogen content of the snake, for example, or indeed its blood sugar, the present findings are more suggestive than helpful in any solution of this complicated problem. Although perhaps the simplest theoretical explanation for this phenomenon of a long-persisting low respiratory quotient would be the possible formation of carbohydrate from fat, such an explanation is obviously less clearly applicable to snakes than to warm-blooded animals. Studies on the chemistry of the blood, with special reference to the blood sugar and to the glycogen content of the snake, may throw light on this perplexing point.

Hári,<sup>1</sup> interpreting the quotients found by Aszódi<sup>2</sup> with his mice in a semi-hibernating condition, considers the technical difficulties carefully and comes to the conclusion that the low quotients found during sleep, coupled with the high quotients in the waking periods, indicate in all probability a formation of glycogen during the period of sleep. Kayser and Ginglinger,<sup>3</sup> using the Haldane method of weighing, consider that they have established the general rule that the respiratory quotients are low with low temperatures and high with higher temperatures, whether one is dealing with the tortoise, the artificially cooled mouse, the rabbit after puncturing the fourth ventricle, the normal pigeon, or the normal guinea-pig, and believe that the respiratory quotient reflects the transformation of carbohydrate into fat and *vice versa*.

To those research workers who have found extraordinarily low respiratory quotients with hibernating animals, this evidence obtained with our 1931 python must be gratifying. In our judgment, however, the situation is different with our python from that with the hibernating animals that have been studied, in that the python data give for the first time clear-cut evidence of an animal organism showing consistently respiratory quotients below 0.70. In most of the investigations on hibernating animals

<sup>1</sup> Hári, P., *Biochem. Zeitschr.*, 1921, **113**, p. 89.

<sup>2</sup> Aszódi, Z., *Biochem. Zeitschr.*, 1921, **113**, p. 70.

<sup>3</sup> Kayser, C., and A. Ginglinger, *Compt. Rend.*, 1927, **185**, p. 1613.

and, indeed, cold-blooded animals the technique has not been impeccable. When, for example, the calculation of a respiratory quotient as low as 0.30 is based upon the accumulation of a few milligrams of carbon dioxide in a train of absorbers weighing several kilograms, the element of possible technical error is too great, even though the absorbers are weighed against dummies. It is believed that the solution of the true respiratory quotient of the hibernating animal can be obtained only by direct gas analysis. Fortunately with the Carpenter gas-analysis apparatus extremely accurate analyses can be made of gases containing one per cent or less of carbon dioxide. Such accurate determinations would rule out completely the possibility of any experimental error and are particularly important when the level of the total metabolism is unusually low and the rate of ventilation of the respiration chamber must be slow.

The uncertainty regarding the nature of the katabolism when respiratory quotients of 0.60 or thereabouts are obtained makes the calculation of the heat production from the measured carbon dioxide exhaled problematical at the lower temperatures. If there is a retention of carbon dioxide, then the metabolism measured by the carbon-dioxide exhalation only, as was the case in the majority of our observations, is really somewhat too low, especially if measured when the temperature is falling or shortly after it has fallen. In prolonged experiments at low temperatures, the latter part of the experiment should not be affected. The reverse situation would be true with rising temperatures, that is, as the temperature rises any carbon dioxide absorbed by the body fluids of the animal and held in solution would be blown off and there would be an increase in carbon dioxide ~~over~~ and above that produced at the moment. Since, however, the total metabolism of the cold-blooded animal is so low at the low temperatures, the amount of carbon dioxide that would have to be absorbed to affect appreciably the respiratory quotient would be such that, with a rising temperature, this amount added to the large amount that would normally be produced by the warmer animal might be so small as not to affect appreciably the quotient. But the caloric value of either carbon dioxide or oxygen when the quotient is below 0.70 has by no means been established. It is not at all impossible that rather considerable errors in the calculation of the heat production may play an important rôle in our cold-blooded data and that all the curves that have been presented in this report for cold-blooded animals would be either materially raised or lowered at the lower temperatures, if the true caloric values of the gaseous products were known. For the time being this must be left an open question. But certainly indirect calorimetry with the cold-blooded animal at 18° or below must be considered to give uncertain results.<sup>1</sup>

The low quotients found with our python at 18° and those occasionally noted with hibernating animals lead to the conclusion that cold-blooded animals at a low temperature are in a somewhat stuporous condition and are undergoing an entirely different metabolic transformation from that prevailing at the higher temperatures. And yet our 1931 python at 18°

<sup>1</sup>This has been clearly emphasized by C. Kayser and A. Ginglinger, *Compt. Rend.*, 1927, 185, p. 1615.

was by no means inert, responded to handling, and on at least one occasion demonstrated rather vigorous activity in an effort to bite the operator (fig. 38, p. 141).

#### CHARACTER OF KATABOLISM DURING DIGESTION

Since the general picture of the respiratory quotient of the cold-blooded animal during fasting is that of a fat katabolism, save under the special conditions outlined above when quotients below 0.70 were found, it can be expected that any changes in the respiratory quotient following feeding will be, in large part, determined by the nature of the food ingested. Consequently, with the snake and the tortoise whose diets consist of protein and of carbohydrate, respectively, dissimilar respiratory quotients are to be expected and, as a matter of fact, are found. Our 1931 python was fed two guinea-pigs in the late afternoon of January 24, and the first respiration experiment thereafter was made on January 27, or 66 hours after food. The respiratory quotient in five well-agreeing periods averaged 0.72 or essentially that of fat. The environmental temperature averaged 31.9° C. (table 55, p. 208). On January 29, or 4 days and 18 hours after food, extraordinarily low and inexplicable quotients, averaging in six periods somewhat less than 0.60, were found at a temperature of 31°. On the next day the respiratory quotient at 31° was again that of fat, and it remained at this level throughout the rest of the study of this animal, except on the days of low environmental temperature mentioned above. The 1931 python therefore showed the anomalous situation of a respiratory quotient averaging 0.72 on January 27 and 0.59 on January 29, although the environmental temperature was 31° on both days. The fact that on January 29 the quotient was determined in six consecutive periods with a carefully controlled gas-analysis apparatus rules out the possibility of any error in the experimental technique and accentuates clearly the extraordinary anomalies in metabolism that can be expected with the python. On none of the days immediately following the ingestion of the guinea-pigs was a respiratory quotient found that might be expected to obtain with an exclusively protein combustion, although one would think that the digestion of two guinea-pigs would have introduced a large protein element into the katabolism that would have been reflected in the respiratory quotient.<sup>1</sup> Until the ninth day after food, that is, on February 2, there is no hint in the determined respiratory quotients of a combustion essentially of protein. On February 2 and 3 the average respiratory quotient is more nearly 0.75 and in but one period is 0.80 actually reached.

In this series of observations on the 1931 python the respiratory quotients were, with the single exception of those on January 29, determined on a sufficient number of consecutive days at the same temperature to show that they could be duplicated under the given conditions and thus served as controls upon each other. The establishment of duplicate quotients on consecutive days was believed to be important, since one can hardly consider

<sup>1</sup>In view of the fact that the end product of protein metabolism with these animals is not that of mammals, the expected respiratory quotients from protein metabolism may not be uncritically taken from mammalian experience.

24 hours as a measurable factor in the life of these animals. The low quotients at 31° on January 29 are wholly inexplicable. Because of the nature of the food eaten, because of the fact that the peak of digestion must have been reached by January 29, that is, 5 days after food, and because of the high environmental temperature, one can conceive of no reason for these low quotients. The accuracy of the gas-analysis apparatus was controlled each day by a careful outdoor air analysis, and the skill of the particular operator who made these determinations, E. L. Fox, is attested by the fact that at this time over 100 outdoor air analyses had been made by him, each representing the first analysis of the experimental day, in which the percentage of oxygen in the air samples was found to vary on the average only  $\pm 0.003$  from the theoretical value for outdoor air of 20.940. Unfortunately, because of the experimental program that the Nutrition Laboratory had under way at the time and because of the preparation of this report, the obtaining of further experimental evidence on this most interesting question was absolutely ruled out and the problem had to be left at this unsatisfactory stage of solution. We are firmly convinced, however, that the quotients as reported in table 55 actually existed.

In general, it may be concluded from the quotients found with the 1931 python that with snakes the respiratory quotient rarely, if ever, rises above 0.80 even during full digestion. This indicates that the katabolism is a protein-fat combustion. Undoubtedly there is a conversion of food protein as well as food fat to body fat, but this is a subtle metabolic difference regarding which our experiments give no information and which needs further study. With the carbohydrate-eating tortoise the picture is quite the opposite. The tortoise consumes a large amount of food at one time, rapidly and freely, without having to be forcibly stuffed. As a result, there is a startling increase in the respiratory quotient which may remain at a high level considerably above 1.0 for one or two days (see pages 368 to 377). General experience with warm-blooded animals, particularly those that can be fed artificially such as the goose, shows that the respiratory quotient may be brought to a high level of approximately 1.4 after a very heavy ingestion of carbohydrate, but that the quotient rapidly falls off until it is below 1.0 and shortly reaches a level characteristic of fat combustion. Our study of the respiratory exchange of the tortoise indicates the actual fat-producing properties of this animal and readily explains the fact that in its natural habitat, when living upon an exclusively carbohydrate diet, it is able to store the large amount of fat that is found in its body. The reaction of the cold-blooded animal to the ingestion of food, therefore, is not (at least at moderately high body temperatures, *i.e.*, about 25° C.) specifically different from the reaction of the warm-blooded animal. The snake and the tortoise are able to burn fat and protein and, with the excessive ingestion of carbohydrate, to convert carbohydrate into fat.

It is startling to find respiratory quotients with the tortoise as high as 1.3 and 1.4 (table 107, p. 371). This is a mystical number. Such quotients were found by Bleibtreu,<sup>1</sup> and the Nutrition Laboratory has found with

<sup>1</sup> Bleibtreu, M., Arch. f. d. ges. Physiol., 1901, 85, p. 345.

stuffed geese that the quotient may be as high as from 1.38 to 1.48. Why is it not higher? Whether any carbon dioxide was formed by fermentation in the case of the tortoise is not known. With geese the Nutrition Laboratory has found that there is no formation of methane when these high quotients appear. It seems logical to argue that the tortoise probably does not produce any carbon dioxide by fermentation, since in at least one case a quotient of 1.3 was found with the tortoise at a low temperature of 18° C.

#### GENERAL CONCLUSIONS REGARDING CHARACTER OF KATABOLISM OF COLD-BLOODED ANIMALS

The cold-blooded animal presents, in general, much the same picture as regards the character of its katabolism as does the warm-blooded animal. It tends to burn fat after a period of fasting, and at times there is a marked rise in the respiratory quotient during prolonged fasting, suggestive of protein-fat combustion. The respiratory quotient of the snake following protein feeding indicates a protein-fat combustion. That of the tortoise following carbohydrate feeding increases enormously. But the most striking feature of the katabolism of these cold-blooded animals is the persistently low respiratory quotient found with the snake at temperatures of 18° or thereabouts. This phenomenon marks the cold-blooded animal as having special properties of its protoplasm to handle metabolites at low temperatures.

#### WATER METABOLISM AND INSENSIBLE PERSPIRATION

The history regarding the water metabolism of many of the large cold-blooded animals, particularly the tortoise, is confusing. The tortoise has a dry, hard exterior, is exclusively a land animal, and frequently lives a long distance from water. These facts, together with the observations of such investigators as Krehl and Soetbeer, have led to the conviction that the tortoise has almost no water metabolism and certainly no loss of water by vaporization, although the excretion of urine may be free. Unfortunately in their classic study, Krehl and Soetbeer relied for the determination of the water lost from these animals upon the use of a hair hygrometer in the ingoing and the outgoing air of their respiration chamber. The Nutrition Laboratory's experience of over two decades with many forms of hygrometer has led us to believe that the hair hygrometer is extremely unreliable for physiological studies in respiration chambers. Fortunately Rubner, in his study of the tortoise, did not use the hair hygrometer but controlled his apparatus carefully by noting the loss in weight of a vessel containing water. His findings are contrary to those of Krehl and Soetbeer and indicate that the tortoise has a liberal vaporization of water.

Our own studies deal with the water metabolism of the cold-blooded animal from two standpoints, the water of vaporization *per se* and the insensible perspiration, but disregard the water in the urine and feces. From our experience with humans and with cattle we are convinced that a close approximation of the total insensible water loss can be obtained by accurate determination of the insensible perspiration. In most of our

measurements of the insensible perspiration of these cold-blooded animals urine and feces were not passed. Hence the data are clear cut and can be taken as an index of the total water vaporized from the body, with the reservation that approximately 85 per cent only of the insensible loss is actually water vapor.<sup>1</sup>

#### AMOUNT OF WATER VAPORIZED

Water vapor as such was determined too infrequently in this research. For the comparison of various animals with respect to their water-vapor output there are available only those observations on boas reported in table 21 (p. 118), and those on the 1931 python reported in table 23 (p. 128). The measured water vapor per kilogram of body weight per 24 hours at rectal temperatures of about 22° to 23° is not far from the same with all the boas, about 2 to 2.5 grams. With boa N, measured at environmental temperatures more nearly 35°, high values of approximately 10 grams were noted. With the 1931 python the closest approach to this high value was 6 grams in two experiments. On the whole, the values at high temperatures for the 1931 python are approximately half those for boa N. The python weighed about 6 kg. and boa N a little over 10 kg. The influence of the shedding cycle on the heat production and the water of vaporization has by no means been clearly established. It is possible that the difference in the results obtained with these snakes is due to the effect of shedding, as boa N was suspected to be approaching the shedding stage. Further than this no comparison between the two series of animals is justifiable. Indeed, among the boas themselves the difference in the results is fairly considerable. Thus, boa N, with a rectal temperature of 35°, vaporized about 10 grams of water per kilogram of body weight per 24 hours, and boa III, with a rectal temperature of 30°, vaporized about 2.5 grams. It is possible that the 5-degree higher temperature of boa N may have increased the water output fourfold. In spite of the absence of sweat glands, there may be with the snake something in the nature of a breaking point in water output comparable to the breaking out of sweat with some of the warm-blooded animals, notably humans.

*Proportion of water vapor leaving the lungs and the skin*—Because of the absence of sweat glands and the demonstrated importance of vaporization of water in the heat regulation of snakes, observations are desirable regarding the proportion of water vapor lost from the lungs and from the skin. The difficulties of separating the water vapor from these two sources, even with humans, can hardly be overestimated.<sup>1</sup> With the snake obviously no head arrangement can be attached, and no direct information on this subject is yet available. It would be possible to compute from the humidity conditions inside the respiration chamber the total amount of water vapor leaving the respiration chamber and, with assumptions as to the probable ventilation of the lungs, one could compute the total water vapor leaving the lungs. The assumptions necessary are, however, too many to justify the calculations. Thus, one must assume, first, that for every cubic centi-

<sup>1</sup> Benedict, F. G., and C. G. Benedict, *Biochem. Zeitschr.*, 1927, **186**, p. 311.

meter of oxygen absorbed from the inhaled air there is a definite ventilation of air, which with humans is not far from 21 c.c. Secondly, it must be assumed that the air leaving the lungs would be saturated at the temperature of the body, and third, it would be necessary to compute the probable degree of humidity of the chamber air from the total water vapor leaving the chamber and the total ventilation. In view of the importance of water vapor as a temperature-regulating medium, further studies on the water vaporized by these animals, with, if possible, a differentiation between the water vaporized from the lungs and that vaporized from the skin, are justifiable.

#### INSENSIBLE PERSPIRATION AS AN INDEX OF WATER VAPORIZED

In these experiments on insensible perspiration with cold-blooded animals it was instantly seen that as the temperature rises the insensible perspiration increases. This is essentially true likewise of the water vapor-

TABLE 113—*Comparison of insensible perspiration of the tortoise and the snake*

Animal	Body weight (total)	Flesh weight	Rectal temperature	Insensible loss per 24 hours	
				Total	Per kg. of flesh weight
	<i>kg.</i>	<i>kg.</i>	<i>°C.</i>	<i>gm.</i>	<i>gm.</i>
Tortoise Y.....	4.4	3.0	21	9.6	3.2
Tortoise Z.....	4.0	2.7	26	9.6	3.6
1931 python.....		5.5	26	23.6	4.3
1931 python.....		6.2	20	2.5	0.4
1931 python.....		6.4	33	46.7	7.3

ized, as directly measured. Indeed, so close is the relationship between water vaporized and insensible perspiration that any discussion of one factor applies with hardly any changes to the other. With both factors there is a pronounced and immediate reaction to the environmental temperature, which is much the same whether the animal is a snake or a tortoise.

Although direct water determinations were not made with the tortoise, there is an unusual interest in any information dealing with the water metabolism of the tortoise on account of the early belief that the tortoise has little, if any, water of vaporization. For the comparison of the insensible loss of our different animals there are available only the measurements on tortoises Y and Z in the 1930 series and those on the 1931 python, reported in tables 103 and 104, (pp. 351 and 352) and in table 22 (p. 124). For convenience these results have been briefly summarized in table 113. Tortoises Y and Z had been fasting about 10 days, the python had been fasting from 4 to 5 days when studied at 26°, about 15 days when measured at 20°, and for only 90 hours after a heavy meal consisting of two guinea-pigs when measured at 33°. The results per kilogram of body weight have been computed with reference to the flesh weight in the case of the tortoises on the assumption that the flesh weight represents two-thirds of the total weight.

In the first experiment with the python at 26° the value of 4.3 grams per kilogram of body weight compares favorably with that of 3.2 and 3.6 grams, computed upon the flesh weight of the two tortoises at temperatures the same or a few degrees lower. The experiment with the python at 20° gives a much lower value, that is, 0.4 gram or one-tenth that at 26°. It is clear that the loss of 7.3 grams at the higher temperature, 33°, noted only 90 hours after a very heavy meal, was affected by the extraordinarily high metabolism of the digestive period. There is little, therefore, in table 113 to suggest that the tortoise, although a dry, land-living animal with a hard shell, has a water metabolism per kilogram of flesh weight materially different from that of the snake.

#### RÔLE OF WATER VAPOR IN HEAT ECONOMY OF COLD-BLOODED ANIMALS

The important rôle played by water in the heat loss of amphibians has been admirably pointed out by Winterstein<sup>1</sup> and by Rubner.<sup>2</sup> With fish, especially, the movement of water through the gills can remove an enormous amount of heat from the body when there is only an inconceivably small difference between the temperature of the water and that of the body. The animal, sunning itself on the beach and becoming too warm in the hot sun, has but to slip into the water in order to lose immediately a large amount of heat by direct conduction. The frog, for example, may make use of water for this purpose, but the frog and other amphibians also have a large vaporization of water from the skin that results in the lowering of the body temperature. The cold-blooded animals such as we studied, with the single exception of the alligator, do not live in the water. Indeed, some of them, as the tortoise, practically never enter the water, at least under experimental conditions. It is perhaps to be regretted that we could not have studied a South American water anaconda, which spends a great deal of time in the water. But entirely aside from the actual amount of water vaporized by these cold-blooded animals and the importance of water vapor as a method of temperature control, we wish to consider here especially the relationship between the water vaporized and the heat loss. The heat production of our cold-blooded animals has been computed from indirect calorimetric measurements. This calculation is admittedly questionable at the lower temperatures, because of the possibility of low respiratory quotients and the unknown caloric value of carbon dioxide at these low quotients. But at temperatures above 25° or thereabouts this possibility does not play any great rôle. The actual amount of heat produced per day by our animals is definitely known. With certain of them, notably the two tortoises studied in 1930 and the 1931 python, frequent measurements of the total insensible perspiration were secured, which of itself is a good index of the water of vaporization, and in the case of some of the snakes the water vaporized was actually determined by absorbing the water vapor from the air current leaving the respiration chamber.

Krehl and Soetbeer have pointed out that many animals actually vaporize more water from their bodies than could possibly be accounted for by

<sup>1</sup> Winterstein, H., *Arch. f. d. ges. Physiol.*, 1908, **125**, p. 88.

<sup>2</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 245.



the heat produced. Each gram of water vaporized from the body at 20° represents the absorption of 585 gram calories. Measurements of the water of vaporization, the heat loss, and the body temperature, with special reference to the temperature of the environment, present a most important study in biological heat values. The general impression derived from analysis of our data is that as a rule most of the cold-blooded animals such as we studied have a rectal or cell temperature somewhat, although not very much, lower than the environment. With snakes the skin temperature is even lower than the rectal temperature, and hence the skin temperature is usually lower than the environment. Under these conditions direct loss of heat by conduction or radiation is inconceivable, and hence it must be concluded that the cold-blooded animal loses all its heat by vaporization of water. Furthermore, as Krehl and Soetbeer have pointed out, the heat corresponding to the water vaporized is so much greater than that produced by the animal that it must be considered that heat is absorbed from the environment to vaporize some of the water.<sup>1</sup> Our experimental data permit a more careful analysis of this situation in the case of the 1931 python, and a comparison of the actual number of calories produced per day and the number of calories required to vaporize the water as actually measured has already been made (see pages 127 to 129).

Cold-blooded animals such as we studied are devoid of sweat glands, and hence the permeability of the skin to the body fluids below the skin must play a rôle. Even the hard, dry skin and the shell of the tortoise are capable of losing water. With the cold-blooded animal, therefore, there is no secretion of water as such through sweat glands, but a normal vaporization of water. Our experimental material was too limited to enable us to state what would be the normal loss in body weight of a dead snake exposed to definite conditions of temperature and humidity, compared with the loss in weight or the actual amount of water vaporized by a live snake under the same conditions. Such a study both at 18° and at 30° should be of considerable importance. It is clear that tortoises, seemingly dry and of a desert habitation, have a much greater insensible loss of water than one would think and that water as such plays an extremely important rôle in their life processes. If the records of the early shipping expeditions to the Galapagos Islands are to be credited,<sup>2</sup> tortoises have been placed in the holds of ships without access to water and have lived for months. It is clear that certain of the tortoises have special water or liquid reservoirs that have played an important rôle in their metabolism. All these points need further study, particularly the quantitative measurement of the water vaporized.

The python and the tortoise have large urinary excretions. No precise knowledge as to their water balance is available. It would not be impossible to arrange experimental conditions so that the water intake could be fairly accurately measured and the water output in feces and urine and through the skin and lungs likewise measured. This we have not been in a posi-

<sup>1</sup> Franz, H. (Biolog. Centralbl., 1930, **50**, p. 158) emphasizes that these animals apparently take up heat according to physical laws and do not seem to possess any spontaneous heat-regulating mechanism.

<sup>2</sup> Van Denburgh, J., Proc. Calif. Acad. Sci., 1914, 4th ser., **2** (I), p. 219.

tion to do. In the Nutrition Laboratory a study of the water vaporized by these animals has been carried out only under two conditions. The insensible perspiration was measured while the animal was suspended in the air from a balance, either in a wire cage or in a metallic box with two openings in it, providing moderate ventilation, and the water of vaporization has been measured while the animal was in the respiration chamber supplied with absolutely dry air.<sup>1</sup> The general picture is that a pronounced lowering in the humidity of the environmental air by rapid ventilation is not accompanied by a marked increase in the water of vaporization.

### DIRECT CALORIMETRY WITH THE SNAKE

The effort to study the metabolism of cold-blooded animals by direct calorimetry has been only partly successful. With an animal immersed in water such as the fish, the micro-calorimeter of Rubner has been most satisfactory.<sup>2</sup> Krehl and Soetbeer used Rubner's calorimeter for amphibians in saturated air, but freely admit the difficulty of employing a calorimeter of that type to measure such small amounts of heat as are produced by even fairly large (one kilogram) cold-blooded animals. With one of our boas (see p. 116) direct calorimetry seemed to indicate that there was no sensible heat. It appeared desirable, therefore, to control this observation with the 1931 python.<sup>3</sup> It was recognized at the outset that the differential calorimeter available in the Nutrition Laboratory, which was designed primarily for warm-blooded animals the size of a goose, small pig, or human infant, could not be used satisfactorily for the measurement of the small amount of heat that would be liberated by even a large cold-blooded animal, such as a 5- or 6-kg. python. But it was believed that at least a qualitative index of the presence of sensible heat could be found with this instrument, which for this particular purpose should be sufficiently delicate. V. Coropatchinsky is responsible for the details.

This differential calorimeter has not, as yet, been described in detail, although its principle has been illustrated both in the small form for infants and the large form for adult humans.<sup>4</sup> The apparatus consists of two thin-walled, metallic, cylindrical vessels over which a powerful blast of air is continually blown, thus insuring that both vessels are bathed by the same volume of air at the same temperature. Inside each can is a large and delicate resistance thermometer. These thermometers form the two arms of a Wheatstone bridge. When the same amount of heat is developed in each can, the Wheatstone bridge is balanced. When a warm-blooded animal is placed in one of the cans (the right-hand can), it is necessary to introduce into the other a definite amount of heat from an electric cur-

<sup>1</sup> Obviously at the relatively slow rates of ventilation used, the air of the chamber always contained some water vapor.

<sup>2</sup> A. V. Hill (Journ. Physiol., 1911, **43**, p. 379) also employed direct calorimetry to study an animal immersed in water, using a calorimeter of his own design.

<sup>3</sup> A direct calorimetric study of the hibernating marmot, an animal approaching the cold-blooded animal, was reported by R. Du Bois in his monumental work on the physiology of the marmot (*Étude sur le Mécanisme de la Thermogenèse et du Sommeil chez les Mammifères. Physiologie Comparée de la Marmotte*, Paris, 1896, p. 113). The calorimeter of d'Arsonval was used.

<sup>4</sup> Benedict, F. G., Bull. Soc. Sci. d'Hygiène Alimen., 1927, **15**, p. 172.

rent through a known resistance, to compensate for the heat produced by the animal and to maintain the Wheatstone bridge at complete balance. The measurement of the electrical energy thus introduced is a direct measure of the sensible heat given off by the warm animal. Provision is made for ventilating the can, to remove carbon dioxide and water vapor from the air current and thus measure the gaseous metabolism as well as the heat given off as water vapor. In the case of the 1931 python it was realized that when the snake was placed in one of the cans, there would be no appreciable amount of sensible heat, but perhaps an actual absorption of heat due to the vaporization of water. A small resistance was therefore placed in the can with the snake, thus making it possible to introduce heat into the chamber where the snake was and maintain the Wheatstone bridge in equilibrium. The snake itself was placed in a wire-mesh cage before being put into the calorimeter.

The first calorimeter experiment with the 1931 python was made on February 16. The temperature of the calorimeter was adjusted at the start to be about 20° C. The temperature of the room in which the snake had been kept had risen to nearly 22° during two or three hours preceding this calorimeter experiment. There was no question, therefore, but what the snake's body temperature was definitely higher than that of the calorimeter when it was placed inside the apparatus. The python weighed approximately 6 kg. On the assumption that the snake has a specific heat of 0.83, or the same as that of man (probably its specific heat is greater than 0.83, since its water content is slightly greater than that of man—see p. 508), a snake of this size would have a hydro-thermal equivalent of not far from 4.5 kg. If 4.5 kg. of water, having a temperature one degree above that of the calorimeter, were placed inside the apparatus, sensible heat would be continually given off by the water until the temperature was equalized. The ventilation rate during the experiment was the slowest that could be maintained. Because of body movements of the snake and because its body temperature was somewhat higher than the temperature of the calorimeter at the start, there was distinct evidence of the loss of sensible heat by the animal during the first 20 minutes, for during this time heat had to be introduced into the compensating can. At the end of this time the Wheatstone bridge showed that the balance was upset, and it became necessary to introduce heat into the chamber containing the snake. This meant that the snake was not only giving off no sensible heat but was actually extracting heat from the environment by the vaporization of water. The amount of heat introduced was not large, but could be measured. As a matter of fact, from 0.045 to 0.10 ampere was passed through a resistance of 81 ohms, previously placed in the snake's chamber. This resistance was connected outside with a milliammeter and a variable resistance. The thermo-junctions indicating the difference between the temperature of the ingoing and the outgoing air likewise caused a slight deflection of the galvanometer, showing that the ingoing air at this time was a little colder than the outgoing air. Theoretically, this meant that cold was being sent into the calorimeter, heat was being brought out and therefore had been absorbed, and hence extra electrical energy had to be introduced into the 81-ohm coil.

The amount of heat introduced remained constant. At 11 a.m., when the snake had been two hours in the calorimeter, the ventilation (which had been at a very slow rate) was stopped. It was thought that possibly the introduction of absolutely dry air, which is a feature of this apparatus, had hastened the vaporization of water, and that, by stopping the ventilation, the air in the chamber would become more and more saturated and less and less water would be vaporized. Since the volume of the chamber was relatively large, 129 liters, for one hour after the ventilation was stopped the amount of heat required to be introduced into the chamber decreased only a little. At noon the functioning of the entire apparatus was stopped, and for one hour no attention was paid to balancing the heat in the two cans. When the ventilation was again started, evidence of a slight amount of sensible heat was again found, since it was necessary to introduce electrical energy into the can not containing the snake. However, after ventilating a relatively short time, it became necessary again to introduce heat into the can with the snake, thus demonstrating anew the fact that the snake was actually absorbing heat from the environment. The temperature at which this calorimeter experiment was made averaged  $21.7^{\circ}\text{C}$ .

In the belief that a similar test at a higher temperature was essential and would be even more striking, the python, on removal from the calorimeter, was placed in a warm room, its body temperature was brought to essentially  $30^{\circ}$ , and it was left there overnight. The next morning, February 17, it was placed in the respiration calorimeter, and there was evidence of a loss of sensible heat continuing for nearly one hour. There was then, for about 30 minutes, essentially a complete balance between the two cans, with no evidence of loss of sensible heat. A little later it was necessary to introduce a slight amount of heat into the left-hand or empty can, and still later, singularly enough, there was a pronounced increase in the amount of heat that had to be introduced into the compensating can to hold the bridge balanced. At first this finding was inexplicable. Then it was noted that the kymograph record of activity gave definite evidence of movement on the part of the snake. This movement had been sufficient to result in the production of a considerable amount of sensible heat. Until this time the ventilation had been at a relatively low rate. Later on the ventilation was increased, in order to introduce a large amount of dry air into the chamber and thus facilitate the removal of water vapor. It was shortly found that no sensible heat could be detected, and it became necessary to introduce heat into the chamber with the snake to compensate for the heat absorbed by the vaporization of water, other than the heat produced by the animal. Even at the higher temperature of  $30^{\circ}$ , therefore, the picture was much the same as that at the lower temperature, depending upon the rate of ventilation or the facility with which water was vaporized inside the chamber. Thus the direct calorimetric measurements with the 1931 python indicated that at  $21^{\circ}$  and at  $30^{\circ}$  no sensible heat was produced by the snake while in repose, but that all the snake's heat was lost by vaporization of water, that somewhat more water was vaporized than that corresponding to the heat given off by the snake, and that extra heat had to be introduced into the snake chamber to compensate for this extra heat required to vaporize the water.

## COMPARISON OF STANDARD METABOLISM, AT DIFFERENT ENVIRONMENTAL TEMPERATURES, OF VARIOUS SPECIES OF COLD-BLOODED ANIMALS IN NUTRITION LABORATORY SERIES

### HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT

Comparison has already been made of the heat production of the various cold-blooded animals in each species that we studied (pp. 213 and 394). It now remains to compare the metabolism of all the different species. The curves indicating the general trend of the standard metabolism of each

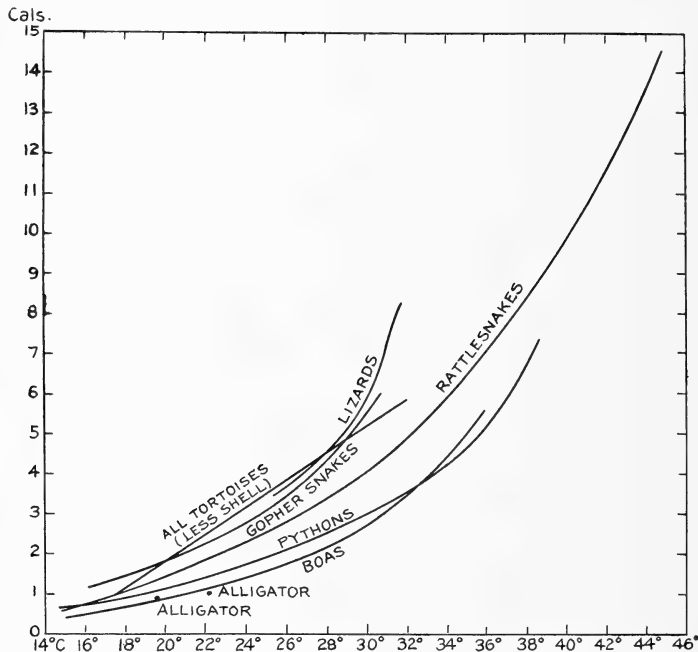


FIG. 99—COMPARISON OF STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS, WITH REFERENCE TO ENVIRONMENTAL TEMPERATURE, OF ALL DIFFERENT SPECIES OF COLD-BLOODED ANIMALS IN NUTRITION LABORATORY SERIES.

species of animal, derived from the plotted data for the standard heat production per kilogram of body weight per 24 hours referred to environmental temperature, have been brought together in figure 99. The metabolism of the tortoises has been indicated on the basis of the weight less shell, and the curve for tortoises represents the giant tortoises as well as the 5-kg. tortoises. In any comparison of these curves it must be remembered that with a number of the animals, notably the boas and to a certain extent the tortoises, there was a wide scatter of the individual plotted points (figs. 54 and 97, pp. 224 and 396), and the propriety of drawing *any* curve to show the general trend of these data was challenged. Another

point to be remembered in making comparisons among the different species of animals is the problem of the correction for the inert shell of the tortoise. The weight of shell of the 5-kg. tortoises is known. The weight of shell of the giant tortoises had to be calculated approximately, as previously outlined (p. 361). These two criticisms must be constantly borne in mind in making any general comparison.

As can be seen from figure 99, the general trend of the standard metabolism with all the animals except the tortoises is distinctly a curve effect. With the tortoises it is a straight-line function. The lizards show the most abrupt rise in metabolism with increasing temperature, and the gopher snakes next. The difference between the various groups of cold-blooded animals on the basis of the heat production per unit of body weight is striking. Thus, the curve for the lizards is for the greater part of its length above the curve for the other animals. The tortoise curve for the most part lies higher than the curves for the other animals. The curve for the boas and the two points for the alligator lie the lowest. The curves for the pythons, boas and rattlesnakes, although at different levels, have about the same general trend upward. The curve for the gopher snakes has much the same inclination as that for the lizards, but these curves suggest that the metabolism of these two species of cold-blooded animals reacts more intensely to the higher temperatures than does the metabolism of the other groups. The metabolism of the tortoises at the lower temperatures approaches that of the rattlesnakes, but at the higher temperatures it is more nearly at the level for the lizards and the gopher snakes. The two points for the alligator are at almost the same level, since they are at temperatures only  $2.5^{\circ}$  apart.

#### HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE

The comparison of the different species of cold-blooded animals on the basis of the standard heat production per square meter of body surface is shown in figure 100. Precisely the same criticisms that applied to the comparison on the basis of the metabolism per unit of weight apply here. In addition, there is the problem as to whether the body surface of the tortoise has been correctly calculated. The curve showing the trend of the metabolism of the tortoises per unit of surface area represents only the 5-kg. tortoises. The data for the giant tortoises have been plotted as individual points, and it will be seen both from figure 100 and by reference to figure 98 (p. 398), that on the basis of body surface it is impossible to draw one curve for all the tortoises, regardless of size. This is in striking contrast to the picture shown by the results per unit of flesh weight, plotted in figure 97 (p. 396). The straight-line curve for the 5-kg. tortoises lies appreciably higher than all the other curves. One might question whether the element of activity might explain this higher level. Our experimental protocols seem to rule this out, for they were very carefully examined and only those observations when activity was absent have been incorporated in figure 100. It is true that the food eaten by these tortoises, particularly just prior to the respiration experiments, was at times not precisely known. On the other hand, a number of the tortoises were kept

continually in the respiration chamber without access to food for several days, so that the influence of food can be considered, at least in those cases, to have been practically eliminated. The two points for the alligator also lie above the curves for the other animals, but the remaining species of animals show singularly close agreement. The curve for the lizards is at a higher level than the curves for the snakes, just as it was on the body-weight basis. There is almost a superimposition of the curves for the

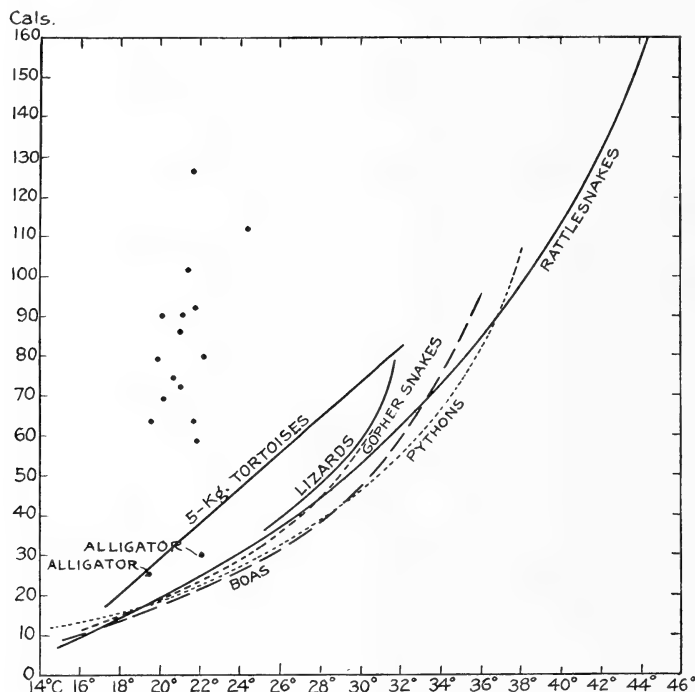


FIG. 100—COMPARISON OF STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS, WITH REFERENCE TO ENVIRONMENTAL TEMPERATURE, OF ALL DIFFERENT SPECIES OF COLD-BLOODED ANIMALS IN NUTRITION LABORATORY SERIES.

Plotted points are for giant tortoises.

gopher snakes, pythons, boas and rattlesnakes, especially at the lower temperatures.

It is conceivable that the metabolism of the rattlesnake might be at one level and that of the boa at another level, although both are snakes. This picture would be much the same as has been found with humans, among whom it has been demonstrated that one race may have a metabolism about 20 per cent below that of another.<sup>1</sup> From figure 100, however, it would appear as if the general trend of the metabolism (the uncertainty of the curve for boas always being held in mind) is strikingly uniform with all the different species of cold-blooded animals, except the tortoises and possibly the alligator. The standard heat production per square meter of

<sup>1</sup> Mason, E. D., and F. G. Benedict, *Indian Journ. Med. Research*, 1931, **18**, p. 75.

body surface is much the same throughout most of the temperature range. The metabolism of the lizards lies higher than that of the snakes between  $30^{\circ}$  and  $32^{\circ}$ , but up until  $30^{\circ}$  there is not a great difference in the various groups. On the other hand, the metabolism of the tortoises is notably greater than that of the other species throughout the entire temperature range, and the giant tortoises especially have a metabolism tremendously higher than any of the other animals. Experiments with the giant tortoises at  $34^{\circ}$  or even higher would have been helpful, to determine whether their relatively high metabolism noted at  $20^{\circ}$  to  $22^{\circ}$  would have persisted.

Since these curves, shown in figures 99 and 100, are for groups of animals, if the tortoises as a group have a specifically higher heat production than the other groups per unit of surface area, this fact can not be disregarded. However, one is instantly impressed with the thought as to whether with the tortoise there is the slightest relationship between the surface area and the heat production and as to whether the picture shown in figure 100 does not challenge the surface-area conception. With the snake and the lizard the curves are grouped more closely together on the body-surface basis than on the body-weight basis, and the question again immediately arises as to whether this has anything whatsoever to do with a thermal relationship. This point will be discussed more in detail subsequently (see pages 470 to 473). Before the calculations for the tortoise can be considered final, we must wait until the weights of shell and of flesh of the larger tortoises have actually been determined. One could assume from the uniformity of results with all the tortoises, when computed per kilogram of flesh weight, that the error in the calculation of the flesh weight of the giant tortoises can not be very great and consequently one may conclude that *the tortoises as a group have a somewhat greater heat production than the other groups of animals.*

### INFLUENCE OF SIZE

In any consideration of the effect of differences in species upon the metabolism of cold-blooded animals, one should not lose sight of the fact that these animals varied in size. Although an attempt has been made to equalize the differences in size by the conventional methods of computing the heat production per unit of weight and per unit of surface area, it must be questioned whether the differences in level of the curves in figures 99 and 100 might be explained, to a certain extent, more by the differences in size than by the differences in species. It would have been ideal if it had been possible to study the metabolism of an alligator, a lizard, a boa, a python, a rattlesnake, a gopher snake, and a tortoise, all of the same weight. The factor of size would then not have been combined with the factor of species. It might be possible to select from our protocols experiments with individual animals weighing approximately the same, but from the wide dispersion of the plotted points already noted for the boas, the comparison of such data would probably lead to false conclusions. Examination of figure 99 (in which the several species of cold-blooded animals have been compared with reference to their metabolism per unit of body weight), however, shows that



the alligator has the lowest heat production. The alligator weighed 53 kg. and, except for the three giant tortoises, was the heaviest of the cold-blooded animals studied. Thus, if the tortoises are disregarded, the largest of the other cold-blooded animals, namely, the alligator, shows the lowest metabolism per kilogram of body weight, just as has been found to be the case with warm-blooded animals. The gopher snakes and the lizards were the smallest of the animals, and their curves on the body-weight basis lie at the highest levels. The rattlesnakes weighed somewhat more on the average than the gopher snakes, and their curve is below that of the gopher snakes. The boas and the pythons weighed on the average more than the other snakes and the lizards, and their curves lie at the lowest level. The flesh weight of the majority of the tortoises was 3 kg., but the curve for these animals is at a high level. The comparison of this curve with the other curves is problematical, however, because of the inclusion of the giant tortoises and the possibility of error in the calculation of the flesh weight of both the small and the large tortoises.

One would infer from this consideration of the body weights of the different species that the heat production per kilogram of body weight was greater with the smaller animals than with the larger. There is a further question whether, if all the species of animals studied had been of the same body weight, there would have been such differences in level of the curves due to a true difference in species. It is unfortunate that more data are not available for the large alligator, particularly at higher temperatures, but this was a specimen that could not well be replaced at the time our experiments were made and the risk of exposing it to higher temperatures could not be taken. Whether the differences in level of these curves are due to differences in size or in species, it is clear that per kilogram of body weight these animals produced notably different amounts of heat. At 30°, for example, the boas (weighing on the average 7 or 8 kg.) produced 2.70 calories per kilogram of body weight and the lizards (average weight 1 kg.) at exactly the same temperature double this amount. This may be an expression of the influence of size or simply a reflection of the mathematical incorrectness of attempting to equalize differences in size by the computation per unit of weight.

This *general* deduction from the comparison of *all* these cold-blooded animals, that the larger the animal the smaller the heat production per kilogram of body weight, is in contradistinction to the finding with the pythons. Of all the different species of animals studied other than tortoises, the pythons had the greatest extremes in body weight. As will be seen by reference to figure 48 (p. 214), the large python had in general the same heat production per unit of weight as the two smaller pythons. Although the most striking contrasts in weight are found with the group of pythons, nevertheless differences in body weight almost equally as large percentagewise were found with some of the boas. Reference to figure 61 (p. 233) will show that with the boas weighing about 4 kg. the heat production per kilogram of body weight was definitely higher than it was with those weighing nearer 12 kg. In this respect the boas differ markedly from the pythons. On the other hand, on the basis of the heat production per

square meter of body surface the 4-kg. and the 12-kg. boas had essentially the same metabolism (see fig. 62, p. 234), whereas among the pythons the large python had much the highest metabolism.

Consideration of the influence of size as reflected by the curves in figure 100, which represent the trend of heat production per unit of surface area with our different species of cold-blooded animals, does not show at all the same situation as the curves on the body-weight basis. Except for the tortoises, the 53-kg. alligator on the surface-area basis has the highest metabolism. The 1-kg. lizards have the next highest metabolism, and the snakes the lowest metabolism, although the curves for the snakes are grouped fairly closely together. The tortoises are completely out of line with the other animals, both the 5-kg. and especially the giant tortoises.

#### RELATIVE MERITS OF HEAT CALCULATIONS PER UNIT OF WEIGHT AND OF SURFACE AREA IN EQUALIZING DIFFERENCES IN SIZE OF ANIMALS

The problem of comparing the metabolism of cold-blooded animals of distinctly different body weights has been handled in two ways. Krogh,<sup>1</sup> whose most careful work especially on small cold-blooded animals can not be challenged, preferred to make his comparisons all on an arbitrary basis founded on the metabolism per unit of body weight. Indeed, he went so far as to compare upon the same chart the metabolism of the curarized dog weighing nearly a kilogram with that of 35-gram frogs and toads and a 9-gram goldfish, therefore presumably assuming that the differences in size were equalized by referring the heat production to the same unit of body weight. Krehl and Soetbeer<sup>2</sup> likewise have made all their comparisons on the basis of the metabolism per unit of weight, although their animals, the lizard, the frog, the alligator, and the *Uromastix*, ranged in weight from 110 to 1380 grams. Rubner,<sup>3</sup> on the other hand, has made his comparisons of cold-blooded animals on the basis of the heat production per square meter of surface area.

Comparison of the curves for our cold-blooded animals indicating the general trend of the metabolism with increasing temperature (see figs. 99, 100) leaves one confused as to the relative merits of the calculations of the heat production per unit of weight and per unit of surface area in equalizing differences in size. So far as the different snakes and the lizards only are concerned, the curves for the heat production per square meter of surface area are far more closely grouped together than are the curves for the metabolism per unit of weight. On the other hand, if the tortoises are taken into consideration, certainly the calculation per unit of weight (less shell) brings the curve for the tortoises, both the 5-kg. and the giant tortoises, reasonably close to the other curves. This is in striking contrast to the picture shown on the per square meter basis, where the curve for even the 5-kg. tortoises lies noticeably above the other curves and the data for the giant tortoises are inconceivably higher than all the curves. On the basis of the metabolism per unit of weight the wider distribution

<sup>1</sup> Krogh, A., *Internat. Zeitschr. f. physik.-chem. Biol.*, 1914, **1**, p. 504; *ibid.*, *The Respiratory Exchange of Animals and Man*, London, 1916, p. 96.

<sup>2</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 611.

<sup>3</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, pp. 222 and 268.

of the snake curves is more than compensated by the fact that all the tortoises and the alligator enter the picture in a relatively reasonable order. From the practical standpoint of attempting to predict what would be the metabolism of these cold-blooded animals, there is little to choose between the two methods of equalizing differences in size, save that the metabolism of the snakes as a whole is probably more uniform on the basis of the heat production per square meter of surface area than it is per kilogram of body weight. The metabolism of the alligator at the two temperatures at which it was measured is noticeably above that of all the other animals per square meter of surface area, except the tortoises. Hence, the metabolism of the alligator and the boas is more closely comparable on the body-weight basis.

If, for purposes of discussion, the snakes are considered as belonging to one family and the attempt is made to combine in one curve the four curves for the different groups of snakes, such an average curve on the body-weight basis would lie not far from that for the rattlesnakes shown in figure 99 and on the body-surface basis not far again from that for the rattlesnakes shown in figure 100. If, therefore, in these two charts, figures 99 and 100, there were only one curve for snakes, one curve for tortoises, and one for lizards, the agreement between the three different species of animals would be as good on the body-weight basis as on the body-surface basis. Indeed, so far as the tortoises are concerned, the agreement would be much better on the weight basis, because the curve here for tortoises represents all the tortoises, both the 5-kg. and the giant tortoises, whereas the curve on the body-surface basis represents only the 5-kg. tortoises.

### EFFECT OF ACCLIMATIZATION

If the trend of the metabolism per kilogram of body weight of the snakes as a group is considered to be represented by the rattlesnake curve and this curve is compared with the curve for tortoises, it is found that the metabolism of the tortoises is definitely above the metabolism of all the snakes over the temperature range at which the tortoises were measured, that is, from about 18° to 32°. The curve for lizards lies, for the most part, above that for the tortoises. This comparison reminds one of the point raised by Krehl and Soetbeer as to the possibility of there being an inherent difference between animals living in the tropics and those in the temperate zone. Thus, Krehl and Soetbeer have compared the heat production of animals from temperate climates (the lizard and the frog) with tropical forms (the alligator and the *Uromastix*) and have found higher results for the former than for the latter at the same environmental temperature. They state: "Das Protoplasma der Tropicthiere hat sich der Umgebungstemperatur angepasst; es arbeitet auch bei den höchsten für die vitalen Functionen günstigsten Temperaturen äusserst sparsam."<sup>1</sup>

Krogh,<sup>2</sup> in discussing the possibility of acclimatization in cold-blooded animals, remarks, "One would expect that animals living at a very low

<sup>1</sup> Krehl, L., and F. Soetbeer, *Arch. f. d. ges. Physiol.*, 1899, **77**, p. 618.

<sup>2</sup> Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, p. 101.

temperature should show a relatively high standard metabolism at that temperature compared with others living normally at a high temperature." Is the protoplasm of the cold-blooded animal adjustable at different temperatures and is there an effect of acclimatization? The difference between the activity of the fish and the snake at a low temperature is marked. The salmon and the trout are capable of lightning-like movements in water at 0° C. The snake, on the contrary, is sluggish at 15°, stuporous at 10°, and wholly inactive at temperatures below that. It is seemingly quiescent at 30°, and yet capable of very rapid movements when striking its prey.

Many of the earlier observations on snakes and lizards did not deal with tropical animals. The cold-blooded animals that we studied were for the most part from the tropics. Undue emphasis has, without doubt, been laid upon the laboratory animal, the frog, which has been studied more than any other cold-blooded animal. Furthermore, its amphibious nature and the large rôle that water plays in its metabolism (as evidenced by the finding that by vaporization of water its body temperature can be lowered 20°)<sup>1</sup> place it in an entirely different category from that of the groups of animals we studied. Our gopher snakes may be considered to represent snakes from a temperate zone. The rattlesnakes came from Texas and probably do not represent, strictly speaking, a tropical species as do the pythons and the boas. From figure 99 (p. 426), it will be seen that these latter have the lowest metabolism of any of the different groups of cold-blooded animals. The rattlesnakes that came from a somewhat cooler climate have a higher metabolism, and the gopher snakes that came from a district farther north have a still higher metabolism.<sup>2</sup>

It must not be overlooked that the differences in size of these various species of animals have already been shown to play a considerable rôle. An effect of the geographical location of the animal therefore can not be considered to be clearly demonstrated, and further analysis of the different levels in the metabolism of our groups of animals on this basis is probably not justifiable.

The contributions made by Baldwin<sup>3</sup> regarding the metabolism of snakes in Iowa, that is, snakes having a habitat comparable to that of our gopher snakes, are to be extended by him to include seasonal differences in the hibernation period as well as sex differences. His experiments thus far published do not lend themselves for direct comparison with our own findings, for apparently he found large differences in the oxygen consumption of his snakes at the same temperature (20° C.) and essentially the same body weight.

Buytendijk's argument, that there is no difference in the metabolism whether or not the snake is from a warm climate, is not conclusive.<sup>4</sup> His snakes were measured at 18° to 19°, at which temperature the metabolism

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 276.

<sup>2</sup> The possible effects of acclimatization with cold-blooded animals are considered theoretically by N. R. Dhar (*Journ. Physical Chem.*, 1926, **30**, p. 480).

<sup>3</sup> Baldwin, F. M., *Proc. Iowa Acad. Sci.*, 1930, **35**, p. 313.

<sup>4</sup> Buytendijk, F. J. J., *Proc. Section of Sci., Royal Acad. Sci., Amsterdam*, 1909, **12**, (I), p. 48; *ibid.*, *Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd.*, 1909, **17**, p. 886.

is very low. The only basis for his statement is the fact that his animals were full grown and had been in captivity for a long time at a temperature of 20°. It is a pity that Buytendijk did not determine the metabolism of his animals at 30° or 35°, and thus see the influence of this tropical temperature upon animals from a tropical source.

### RATE OF METABOLIC REACTION OF COLD-BLOODED AND WARM-BLOODED ANIMALS TO CHANGES IN ENVIRONMENTAL OR BODY TEMPERATURE

The ability of the warm-blooded animal to resist the influence of environmental temperature has been definitely established. By means of protective covering, such as hair or feathers, and by means of activity the warm-blooded animal can, under ordinary conditions, combat the effect of cold and hold its body temperature reasonably constant. With increasing cold there is usually an increase in the metabolism. This increase may be brought about by two independent processes, (1) the so-called "chemical" stimulus, and (2) body movement or activity, as in shivering and tension of the body. Sharp discrimination between these two processes is not ordinarily made. The grosser body movements, such as shivering, can be recorded graphically. Obviously, since muscular activity is known to increase metabolism, *any* muscular activity, particularly if visible, must in part account for the increased metabolism of the warm-blooded animal following the first stages of a falling environmental temperature. When the environment is extremely cold and particularly if the animal is not well protected or the means of protection has been artificially removed, as was done in the experiments of Giaja,<sup>1</sup> the rectal temperature finally falls and the metabolism becomes much lower. It is difficult to determine the exact level to which the body temperature has fallen at that moment when the warm-blooded animal can no longer combat the cold and therefore dies. Aside from exposure to extreme cold, the environmental temperature has but a moderate effect upon the metabolism of most warm-blooded animals.

The effect of heat upon warm-blooded animals is likewise, in large part, compensated by their automatic means of protection, as instanced by the laying down of the feathers close to the body in the case of birds, the smoothing of the fur in the case of fur-bearing animals, the stretching out of the dog to expose more of its body surface and the opening of its mouth and panting to permit extreme vaporization of water from the tongue, and in the case of man the profuse exudation of sweat which results in a greatly increased vaporization of water and hence an increased heat loss. Under normal conditions, therefore, the temperature of the warm-blooded animal and similarly its metabolism are not appreciably altered by heat. On the contrary when, notwithstanding any of these automatic means of protection against excessive heat, or when by reason of any internal process, such as fever, the temperature of the body cells is

<sup>1</sup> Giaja, J., *Ann. de Physiol.*, 1925, **1**, p. 596.

increased, there is a greater heat production. During hibernation, when the temperature of its surroundings is low, the rectal temperature of the warm-blooded animal decreases. During the awakening process both body temperature and metabolism increase. The effect of curare is to lower the rectal temperature and the metabolism, when the environmental temperature is low. The section of the spinal cord has a like effect, if the environment is cold. The environmental temperature therefore has a pronounced effect upon warm-blooded animals under these special conditions. When the environmental temperature for any reason affects the cell temperature of the warm-blooded animal, there is an increase in heat production accompanying an increased cell temperature. In this respect warm-blooded animals resemble closely cold-blooded animals, for with all cold-blooded animals the higher the temperature of the environment or the cell temperature (which closely approximates that of the environment), the greater is the heat production. With warm-blooded animals the range over which the rectal temperature can change and the animal not die is relatively small. A fever of a few degrees is tolerated, but beyond that the animal usually dies. Similarly with extreme cold, death occurs. On the other hand, with cold-blooded animals any change in environmental temperature between  $0^{\circ}$  and  $30^{\circ}$  or even  $40^{\circ}$  is immediately reflected in a change in the metabolism, but without the death of the animal except under certain conditions at the extremes in temperature.

The quick and precise reaction of the heat production of the cold-blooded animal to changes in temperature has been illustrated graphically in the numerous standard metabolism curves shown in the figures in the preceding pages of this report. This reaction to temperature may also be expressed mathematically. What is the rate of increase in the metabolism of the cold-blooded animal with increasing temperature? Is it regular or irregular? Does it follow any law? From the metabolism curves obtained with practically all our animals a general statement can be made that, as the environmental temperature increases, the heat production increases. The curves, however, are not all precisely of the same order and must be subjected to mathematical analysis. This mathematical analysis can be made in two ways. In recent years special emphasis has been laid upon the comparison between the rate of acceleration of the life processes over a definite temperature interval and the rate of acceleration of well-known chemical processes. Thus, van't Hoff and Arrhenius have found that the rate of increase of chemical reactions and many physiological processes with increasing temperature may be represented by an algebraic formula, the solution of which, in general, indicates that for every 10-degree increase in temperature there is a doubling or trebling of the chemical or physiological reaction. This has been popularly expressed as the " $Q_{10}$  law" or by Kunitz as the "R. G. T. rule."<sup>1</sup> The calculation of the  $Q_{10}$  is simple,<sup>2</sup> if the metabolism has been measured at temperatures exactly

<sup>1</sup>Kunitz, A., *Die Biochemie in Einzeldarstellungen, I: Temperatur u. Lebensvorgänge*, Berlin, 1915.

<sup>2</sup>In the calculations of the  $Q_{10}$  from the metabolism curves for our various cold-blooded animals, as well as in the application of the calculated  $Q_{10}$  to the prediction of metabolism and in the consideration of logarithmic plots, we were greatly aided by the counsel and judgment of Professor E. B. Wilson of the Harvard School of Public Health. We wish to express our thanks to him for his sustained interest in this problem.

10 degrees apart. For example, if the heat production of a snake has been determined at 20° and again at 30°, the higher metabolism at 30° may be divided by the lower metabolism at 20° and the resulting quotient, which is usually somewhere between 2 and 3, is the so-called " $Q_{10}$ ." When the metabolism has been determined at two temperatures that are more or less than 10 degrees apart, the  $Q_{10}$  may be calculated with reasonable accuracy by dividing the metabolism at the higher temperature by that at the lower temperature, then dividing this quotient by the number of degrees in the temperature interval under consideration, and multiplying this result by 10.

The second method of mathematical analysis of the reaction of the metabolism to temperature is the calculation of the percentage change in heat production per degree change in environmental temperature, either on the basis of an increasing or a decreasing temperature. If the metabolism has been measured at 10° and then again at 20°, for example, what is the percentage rate of increment for each degree? This percentage increment is obtained by dividing the increase in metabolism, that is, the difference between the metabolism at the lower temperature and that at the higher temperature, by the metabolism at the lower temperature and by the number of degrees in the particular temperature interval studied. Similarly, the percentage decrease may be computed by dividing the difference in metabolism at two given temperatures by the metabolism at the higher of the two temperatures. The percentage change in metabolism, more commonly computed as the percentage increment, differs from the  $Q_{10}$  in that it represents the percentage change in metabolism above or below a given baseline for a 1-degree temperature interval and not, as the  $Q_{10}$ , the relative magnitude of the metabolism at a given temperature 10 degrees above a given baseline. One should not confuse the  $Q_{10}$ , which represents a 10-degree interval, with the percentage increment, which represents a 1-degree interval. Thus, the increment for one degree may be 10 per cent but the  $Q_{10}$  for ten degrees will not be 1.0 (100 per cent) but perhaps 2.5 (250 per cent) because, as Martin<sup>1</sup> has so aptly expressed it, the  $Q_{10}$  represents a "compound interest" effect. Both forms of expression will be considered in this report.

The rate of acceleration in chemical reactions and physiological processes has been extensively reviewed by Kanitz,<sup>2</sup> Snyder,<sup>3</sup> and especially by Bélehrádek.<sup>4</sup> In general it has been found that the  $Q_{10}$  is between 2.0 and 3.0 with chemical as well as physiological processes, but that neither the percentage increment nor the  $Q_{10}$  remains constant over a wide temperature range, particularly in physiological processes. As the temperature rises, the rate of increase in the chemical or physiological process for a 10-degree temperature interval becomes somewhat less. The  $Q_{10}$  between 5° and 15°, for example, would be much larger than that between 25° and 35°, perhaps of the order of 3.9 or 4.0 at the lower temperature level and as small as 2.1 at the higher scale. The metabolism curves for our cold-

<sup>1</sup> Martin, C. J., *Lancet*, 1930, p. 561.

<sup>2</sup> Kanitz, A., *loc. cit.*

<sup>3</sup> Snyder, C. D., *Amer. Journ. Physiol.*, 1908, **22**, p. 309.

<sup>4</sup> Bélehrádek, J., *Biol. Rev., Cambridge Philos. Soc.*, 1930, **5**, p. 30.

blooded animals, when subjected to mathematical analysis, show clearly that, in conformity with the rate of reaction of other physiological processes, the values for the percentage increment and the  $Q_{10}$  depend entirely upon the temperature interval selected. The change in metabolism calculated for the temperature interval between 10° and 20° may be one value, that for the interval between 20° and 30° another value, and that between 10° and 30° an altogether different value. The  $Q_{10}$  and the percentage increment are, moreover, by no means constant even with the same species. Sufficient experimental evidence is not yet at hand to determine whether they are uniform for the same animal, because usually the experimental data on any one animal have been secured in a short period of time, frequently on one or two days over the entire temperature range. Hence the chance variations that might appear in the ordinary course of a week, a month, or a year are not noted and the  $Q_{10}$  is known only for the particular two or three days of the experimental period.

In the comparisons that are to be made subsequently regarding the metabolism of cold-blooded and warm-blooded animals, use will be made of the temperature coefficients calculated both on the basis of the percentage increase or decrease in heat production above or below the heat production at a given temperature and on the basis of the  $Q_{10}$ . In the first place, an analysis will be made of the temperature coefficients obtained with our own cold-blooded animals over the actual temperature ranges studied, to determine whether these coefficients are consistently the same or strikingly different at the various temperature intervals with the various groups of animals. Secondly, the temperature coefficients found with our cold-blooded animals will be compared with those found on other cold-blooded animals by other investigators. In the third place, the temperature coefficients for cold-blooded animals, such as those measured by us, will be compared with the accepted temperature coefficients for warm-blooded animals and chemical reactions in general. An important practical application of the temperature coefficient may be made in considering the fundamental problem of what would be the probable metabolism of a cold-blooded animal if it had been measured at the cell temperature obtaining with warm-blooded animals, that is, about 37°. As has already been pointed out, it was impracticable with many of these expensive animals to subject them to 37°. Frequently measurements were made over a wide temperature range to as high as 30°, and it is proposed to use the probable temperature coefficient to predict what would be the metabolism of these animals at 37° C.

#### PERCENTAGE CHANGE IN METABOLISM WITH CHANGING ENVIRONMENTAL TEMPERATURE

The percentage change in the standard metabolism of our cold-blooded animals per degree change in environmental temperature<sup>1</sup> has been computed both on the ascending and the descending scale, based upon the various smoothed curves shown in figures 99 and 100 (pp. 426 and 428),

<sup>1</sup> Here, as elsewhere, with these cold-blooded animals the environmental temperature and body temperature are assumed to be essentially the same.



indicating the general trend of the metabolism with changing temperature for each species of animal studied. The results have been summarized in table 114. Although the values in this table for the heat production per square meter of body surface, and with the tortoise also the heat production per kilogram of flesh weight, may be called in question, owing to the uncertainty regarding the calculations of the surface areas of the different animals and the weight of shell of the tortoise, the relative worth of the values at the different temperatures can hardly be questioned. Hence the comparison of the percentage changes in metabolism at the different temperatures is justifiable, even if the basis of the calculation may be questioned. In the case of the rattlesnakes and the tortoises, the percentage change in metabolism, both on the ascending and the descending scale and whether referred to unit of body weight or unit of body surface, becomes smaller the higher the temperature scale. In the case of the other animals, however, there is not much change in the percentage values as the temperatures become higher. The percentage increase or decrease in any given temperature interval is not precisely the same on the body-weight and the body-surface basis, probably due in large part to the uncertainty in sketching the smoothed curves from which these values were computed.

In table 114 the calculations of the percentage changes have been restricted to temperature intervals of 10 degrees, save in the case of the lizards, where the interval is only 5 degrees. It is important, however, to note the effect upon these calculations of considering larger temperature intervals, for in the literature such calculations have frequently been based upon a much wider interval. A typical case may be illustrated with the rattlesnakes, which were studied at temperatures between 15° and 44°. The heat production per kilogram of body weight per 24 hours at 15° is 0.65 calorie. At 44° it is 13.55 calories. The difference in heat production is 12.90 calories. Referring this difference to the lower heat production, that is, 0.65 calorie, one sees that there is an increase in metabolism of 1985 per cent for a temperature interval of 29 degrees, or an increase of 68.4 per cent per degree. Inspection of the values in table 114 for the increase per degree, where the 10-degree intervals are used, shows that they range on the body-weight basis from only 12.8 to 29.1 per cent. The danger of calculating the percentage increment when measurements are made only over a wide temperature interval can thus hardly be over-emphasized.

The chief use of these temperature coefficients is to compute the probable metabolism of an animal at a temperature either above or below the actual temperature studied. Thus, the metabolism of animals measured at 21° has been "corrected" to 16°. Our own desire is to "correct" the metabolism of animals at 30° to 37°. Hence we are particularly interested in the temperature coefficients on the increasing scale. From table 114 one could draw the general conclusion that with temperature intervals of not over 10 degrees, the heat production of these cold-blooded animals increased approximately 20 per cent per degree on the ascending scale and decreased approximately 7 per cent per degree on the descending scale. The application of these percentages in "correcting" the metabolism to a

different temperature level must take into account the fact that they hold only for 10-degree intervals, and that if a wider interval were considered, the increase in metabolism, for example, might be as large as 70 per cent.<sup>1</sup>

TABLE 114—Percentage change in metabolism of cold-blooded animals per degree change in environmental temperature, and the  $Q_{10}$

Animal and temperature interval	Heat produced per kg. per 24 hours					Heat produced per sq. m. per 24 hours				
	At lower temperature	At higher temperature	Per cent increase per degree	Per cent decrease per degree	$Q_{10}$	At lower temperature	At higher temperature	Per cent increase per degree	Per cent decrease per degree	$Q_{10}$
Boas:	<i>cal.</i>	<i>cal.</i>								
16° to 26°	0.55	1.80	22.7	6.9	3.3	9.8	31.0	21.6	6.8	3.2
26° to 36°	1.80	5.65	21.4	6.8	3.1	31.0	96.0	21.0	6.8	3.1
Rattlesnakes:										
15° to 25°	0.65	2.54	29.1	7.4	3.9	7.5	33.7	34.9	7.8	4.5
16° to 26°	0.77	2.80	26.4	7.3	3.6	9.6	37.2	28.8	7.4	3.9
24° to 34°	2.30	5.95	15.9	6.1	2.6	31.0	74.2	13.9	5.8	2.4
26° to 36°	2.80	7.10	15.4	6.1	2.5	37.2	86.0	13.1	5.7	2.3
34° to 44°	5.95	13.55	12.8	5.6	2.3	74.2	157.0	11.2	5.3	2.1
Gopher snakes:										
17° to 27°	1.20	3.67	20.6	6.7	3.1	12.3	39.0	21.7	6.8	3.2
18° to 28°	1.40	4.02	18.7	6.5	2.9	14.2	44.0	21.0	6.8	3.1
20° to 30°	1.82	5.30	19.1	6.6	2.9	18.0	58.0	22.2	6.9	3.2
Pythons:										
16° to 26°	0.70	2.10	20.0	6.7	3.0	13.0	32.0	14.6	5.9	2.5
24° to 34°	1.70	4.20	14.7	6.0	2.5	27.0	66.9	14.8	6.0	2.5
26° to 36°	2.10	5.18	14.7	5.9	2.5	32.0	82.0	15.6	6.1	2.6
28° to 38°	2.54	6.70	16.4	6.2	2.6	38.5	106.0	17.5	6.4	2.8
Lizards:										
26° to 31°	3.65	7.24	19.7	9.9	3.9	39.0	70.0	15.9	8.9	3.2
Tortoises <sup>1</sup>										
18° to 28°	1.15	4.50	29.1	7.4	3.9	20.0	64.2	22.1	6.9	3.2
22° to 32°	2.48	5.84	13.5	5.8	2.4	37.7	81.9	11.7	5.4	2.2

<sup>1</sup> Calculations based on flesh weight. All tortoises included in calculations on body-weight basis; only the 5-kg. tortoises included in calculations on surface-area basis.

In the literature are reported a few metabolism measurements on cold-blooded animals in which we are particularly interested, that permit the calculation of the percentage changes in metabolism with variations in environmental temperature. Thus, Regnault and Reiset<sup>2</sup> measured lizards

<sup>1</sup> This large value is due to the arithmetical method of computing the percentage increase in metabolism, namely, by referring the difference in heat production at the two temperature extremes to the small heat production at the lower of the two temperatures.

<sup>2</sup> Regnault, V., and J. Reiset, *Annales de Chim. et de Phys.*, 1849, 3d ser., **26**, p. 299.

weighing approximately 21 grams each, at 7.3°, 14.8° and 23.4° C. The increase in heat production per degree between 7.3° and 14.8° was 21.5 per cent and between 14.8° and 23.4° was 22.8 per cent. The corresponding calculations on the decreasing scale were 8.2 and 7.7 per cent, respectively. Krehl and Soetbeer<sup>1</sup> measured their four animals, the lizard, the frog, the alligator, and the Uromastix, at 25.3° and at 37°. The increase in metabolism per degree for this temperature interval of 11.7° was with the lizard 7.5 per cent, with the frog 7.7 per cent, with the alligator 4.9 per cent, and with the Uromastix 4.7 per cent. Rubner's<sup>2</sup> frog was measured at 3°, 20° and 30° C. The increase in heat production between 3° and 20° was 8.1 per cent, and between 20° and 30° it was 0.7 per cent. On the descending scale between 20° and 3° the decrease in metabolism was 3.4 per cent per degree and between 30° and 20° it was 0.6 per cent. His tortoise was measured at 20°, 30° and 37°. Between 20° and 30° the increase in metabolism per degree was 15.0 per cent and between 30° and 37°, 3.3 per cent. The decreases in metabolism were 6.0 and 2.7 per cent per degree, respectively. Rubner also made measurements on goldfish at 16.6° and 21.8°, and he computes the increase in heat production per degree as 9.6 per cent. Likewise his sticklebacks were measured at 18° and 23.5°, and here again for each degree rise in temperature Rubner found an increase in metabolism of essentially 9 per cent. By reference to table 114 it can be seen that, for the most part, our percentage increases are much larger than those obtained by others, save the values of Regnault and Reiset. In all such comparisons, especially since the temperatures at which the earlier measurements on cold-blooded animals were made range from 3° with Rubner's frog to 37° with the animals of Krehl and Soetbeer, it is obvious that the factor of activity at the higher temperatures and the factor of stupor, if not indeed rigidity, at the lower temperatures must play some rôle.

With warm-blooded animals under normal conditions and with warm-blooded animals subjected to either curare, excessive cooling, section of the spinal cord, or hibernation, earlier researches have usually shown differences in metabolism at different temperatures, but rarely are the metabolism values expressed in terms of percentage increment. The marmots studied by Mareš<sup>3</sup> were measured only at two extremes of temperature, and the danger of using a wide temperature interval in computing the percentage change in metabolism has already been pointed out. On the other hand, with Krogh's curarized dog,<sup>4</sup> with the pithed rabbit of Krarup,<sup>5</sup> and with the curarized rabbits of Velten,<sup>6</sup> data are available that permit the calculation of the percentage changes. Bearing in mind that the temperature interval should not be too large and that the length of the interval affects profoundly the percentage factor, we have incorporated

<sup>1</sup> Krehl, L., and F. Soetbeer, Arch. f. d. ges. Physiol., 1899, **77**, p. 611.

<sup>2</sup> Rubner, M., Biochem. Zeitschr., 1924, **148**, p. 277.

<sup>3</sup> Mareš, F., Bohemian Arch. Med., Journ. Advancement Med. Sci., Prague, 1889, **2**, pp. 458-527; *ibid.*, Compt. Rend. Soc. de Biol., 1892, 9th ser., **4**, p. 313.

<sup>4</sup> Krogh, A., Internat. Zeitschr. f. physik.-chem. Biol., 1914, **1**, p. 491.

<sup>5</sup> Krarup, F. C., *The Influence of the Surrounding Temperature on the Respiratory Exchange and the Production of Heat*, Dissert., Copenhagen, 1902. (In Danish.)

<sup>6</sup> Velten, W., Arch. f. d. ges. Physiol., 1880, **21**, p. 361.

in table 115 the calculations of some of the percentage increments shown by the data of Krogh, Krarup and Velten, based upon temperature intervals in many cases of about 10 degrees. This makes the calculations in a sense comparable with the values reported for our cold-blooded animals in table 114 which are, with one exception, all on the basis of a 10-degree temperature interval. The calculations have been made both on the ascending and the descending scale. In general the values selected from Velten's series are much lower than the others on the increasing scale.

TABLE 115—Percentage change in metabolism with increasing and decreasing temperatures—Warm-blooded animals

Investigator	Animal	Temperature interval <sup>1</sup>	Per cent increase per degree <sup>2</sup>	Per cent decrease per degree <sup>2</sup>
Krogh <sup>3</sup> .....	Curarized dog...	14.1° to 22.7°	14.2	6.4
		28° to 32.2°	6.7	5.2
		14.1° to 39.9°	16.2	3.1
Krarup <sup>4</sup> .....	Pithed rabbit....	26° to 36°	37.6	7.9
Velten <sup>5</sup> .....	Curarized rabbit.	37.2° to 30.7°	13.2	7.1
		38.3° to 27.6°	11.3	5.1
		38.3° to 26.6°	16.8	5.7
		38.1° to 30.8°	6.8	4.5
		38.1° to 26.7°	11.6	5.0
		38.4° to 29.3°	10.4	5.3
		38.4° to 24.5°	10.0	4.2
		38.1° to 23.2°	5.3	6.0
		30.7° to 26.3°	9.4	6.7
		30.7° to 25.0°	1.5	1.4
		26.6° to 36.6°	18.2	6.5
Average....	.....	.....	12.6	5.3

<sup>1</sup> Rectal temperatures in all instances.

<sup>2</sup> Percentage increase calculated by deducting metabolism value at lower temperature from that at higher temperature, dividing difference by result at lower temperature, and then by number of degrees in temperature interval. Percentage decrease calculated by dividing difference between two metabolism measurements by result at higher temperature and by number of degrees. By this method of calculation obviously the percentage increase will be larger than the percentage decrease because computed upon a lower baseline.

<sup>3</sup> Krogh, A., *Internat. Zeitschr. f. physik.-chem. Biol.*, 1914, **1**, p. 491.

<sup>4</sup> Krarup, F. C., *The Influence of the Surrounding Temperature on the Respiratory Exchange and the Production of Heat*, Dissert., Copenhagen, 1902. (In Danish.)

<sup>5</sup> Velten, W., *Arch. f. d. ges. Physiol.*, 1880, **21**, p. 361.

These percentages are based upon values selected at random from his data for his individual rabbits. Velten, himself, reports an average percentage decrease in oxygen consumption for all his animals of not far from 5 or 6 per cent per degree fall in body temperature, over short temperature intervals. On the increasing scale his average percentages vary from 2.2 to 19.5.

The averaging of percentage figures varying as widely as from 1.5 to 37.6 is hardly permissible, and yet if such an average were made for the percentage increments in table 115 it would be 12.6 per cent per degree.

On the decreasing scale the general average would be 5.3 per cent, or somewhat less than half of the percentage increment. With our series reported in table 114 the values vary less widely, and the percentage increase per degree is on the average more nearly three times the percentage decrease. It is clear that the variation in the values reported in table 115 is too great not to demand further experimentation. Undoubtedly the apparently greater regularity of the percentages in our series in table 114 is due to the fact that these were all based upon smoothed curves. The average percentage increase for the Nutrition Laboratory series is about 20 per cent and the average percentage decrease about 7 per cent, as compared with the averages of 12 and 5 per cent, respectively, calculated for the animals of Krogh, Krarup, and Velten. The averages in the latter case, however, are made up of much more widely differing individual values. On the ascending scale the difference between 20 and 12 per cent might be considered significant, as indicating a real difference in the reactivity of cold-blooded and warm-blooded animals, that is, indicating that cold-blooded animals react more intensely to temperature changes than do warm-blooded animals that have been curarized or pithed. Since the calculations on the decreasing scale, however, are essentially identical in both cases, it can only be concluded that there are undoubtedly no profound differences in the rate of metabolic reaction of cold-blooded animals and warm-blooded animals, under these special conditions, to changes in body temperature. The *rate* of the metabolic reaction must not be confused, however, with the *absolute level* of the metabolism, which, as will be shown later (pp. 478 to 493) is much greater with warm-blooded animals whose body temperature is lowered under special conditions than is that of cold-blooded animals at the same cell temperature.

Rubner<sup>1</sup> makes a general statement that with warm-blooded animals the metabolism is increased from 2 to 3 per cent for each degree fall in *environmental* temperature. Du Bois, although treating the subject of fever chiefly from the standpoint of the  $Q_{10}$ , concludes that the average rise in heat production is about 13 per cent for each degree (Centigrade) rise in *body* temperature.<sup>2</sup> Special consideration of the temperature factor, however, may best be given when the more scientifically exact coefficient, commonly expressed as the  $Q_{10}$ , is treated.

#### THE $Q_{10}$ AS AN EXPRESSION OF REACTION OF METABOLISM TO CHANGES IN ENVIRONMENTAL TEMPERATURE

The values for  $Q_{10}$  for our own species of cold-blooded animals over the different temperature ranges at which they were studied have been computed and also summarized in table 114. These calculations show that with the rattlesnakes and the tortoises the  $Q_{10}$  decreases as the temperature rises. This finding is in common with other biological observations, especially those by Krogh. With the other groups of animals there is little

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 238.

<sup>2</sup> Du Bois, E. F., *Basal Metabolism in Health and Disease*, Philadelphia, 2d ed., 1927, p. 389.

change in the  $Q_{10}$ . All the values for  $Q_{10}$  lie between 4.5 and 2.1. They are presented here chiefly as evidence of the general applicability of the " $Q_{10}$  law" or the "R. G. T. rule" to the metabolic processes of these large cold-blooded animals.

The values for  $Q_{10}$  for the tortoises on the body-weight basis (flesh weight) are based upon the curve in figure 97 sketched through the plotted points for all the tortoises, both the 5-kg. and the giant tortoises. The values on the body-surface basis represent only the 5-kg. tortoises. It is conceivable that, because the giant tortoises were studied at the lower temperatures and only the 5-kg. tortoises at the higher temperatures, the level of the curve might be greatly lowered at the lower temperatures by the data for the giant tortoises, on the ground that large animals have a smaller heat production per kilogram of body weight than do small ones. As a matter of fact, if the data for all the giant tortoises were omitted from figure 97 and the curve drawn through the plotted data only for the 5-kg. tortoises, the location of the curve would not be greatly changed from its present position.

The relatively few cold-blooded animals that have been studied of a size and nature comparable to ours, for which data are available for computing the  $Q_{10}$ , have been cited on page 440 in the discussion of the percentage increments.<sup>1</sup> Expressing these values on the  $Q_{10}$  basis, we note that Regnault and Reiset found with their lizards a  $Q_{10}$  of 3.5 between 7.3° and 14.8°, and a  $Q_{10}$  of 3.4 between 14.8° and 23.4°. Krehl and Soetbeer found between 25.3° and 37° a  $Q_{10}$  with the lizard and the frog of 1.6, with the alligator of 1.3, and with the *Uromastix* of 1.3. Rubner's frog between 3° and 20° gave a  $Q_{10}$  of 1.4 and between 20° and 30° of 1.1. His tortoise between 20° and 30° gave a  $Q_{10}$  of 2.5 and between 30° and 37° of 1.8. Aside from the values for the lizards of Regnault and Reiset and the tortoise of Rubner between 20° and 30°, all the other values for  $Q_{10}$  lie below our lowest value, which is 2.1. The generally prevailing low values for  $Q_{10}$  averaging, roughly speaking, about 1.5 are comparable to those of Bodine,<sup>2</sup> who found from 0° to 10° a  $Q_{10}$  of 1.1 and from 15° to 25° of 1.5. Bodine's values are extraordinarily low for biological processes in general and of uncertain value for comparison with these larger cold-blooded animals, since his results were obtained on insects.

The general uniformity of the values for  $Q_{10}$  in table 114 shows immediately that the use of the  $Q_{10}$  in the prediction of the metabolism at a higher temperature than that at which it was actually measured would be justifiable, with probably a smaller percentage error in the projection upward than downward. As will be seen later, however, we found after consideration of the values for  $Q_{10}$ , that the projection (by inspection) of our curves showing the general metabolic trends would be fully as justifiable and perhaps give values with a somewhat higher degree

<sup>1</sup> According to Riddle's studies (Amer. Journ. Physiol., 1909, **24**, p. 447) the rule of van't Hoff applies to the digestive processes in living cold-blooded vertebrates within certain not very wide ranges of temperature, the average of eight valid coefficients being 2.62.

<sup>2</sup> Bodine, J. H., Journ. Expt. Zool., 1921, **32**, p. 159.

of probability (page 447). The danger of determining the  $Q_{10}$  value for a physiological process over one or more temperature intervals and then using the average result over a wide range of temperatures has been clearly pointed out by Krogh.<sup>1</sup>

Owing to the fact that the warm-blooded animal undergoes temperature changes only under special conditions, such as those outlined on page 435, and rarely is subjected to a change in cell temperature amounting to 10 degrees, the  $Q_{10}$  has seldom been considered for warm-blooded animals other than those under curare, section of the spinal cord, or hibernation. Du Bois concludes from his extensive series of measurements with humans in fever that the  $Q_{10}$  for the increase in metabolism during fever corresponds to a value of 2.3.<sup>2</sup> In considering the influence of changes in temperature upon the metabolism of warm-blooded animals and particularly in computing the temperature coefficients for comparison with those of cold-blooded animals, one must bear in mind that with cold-blooded animals the temperature of the environment is essentially the cell temperature, and the computation of the  $Q_{10}$  is based upon a change in metabolism produced by a change in the cell temperature of the animal. In warm-blooded animals changes in cell temperature are induced by fever, curare, section of the spinal cord, hibernation, and excessive cooling, such as that employed by Giaja.<sup>3</sup> The  $Q_{10}$  computed under such conditions must not be confused with the increment in metabolism reported for warm-blooded animals when the *environmental* temperature falls and it is found, for example, that there is an increase in heat production of about 2 or 3 per cent per degree decrease in temperature. This percentage increment also obtains with birds. With the albino rat the increase in metabolism has been repeatedly observed to be about 5 per cent per degree decrease in environmental temperature. But in these particular instances we are dealing with the reaction of the warm-blooded organism to changes not in cell temperature but in environmental temperature, a reaction which brings into play Rubner's "chemical heat regulation."

Du Bois emphasized that the  $Q_{10}$  law obtains with man in fever.<sup>2</sup> With the curarized dog of Krogh an approximation of the  $Q_{10}$  law was noted, and among our own cold-blooded animals the  $Q_{10}$  law obtains for the most part. It might readily be argued therefore that, since the  $Q_{10}$  for cold-blooded animals is of the same order of magnitude (between 2 and 3) as the  $Q_{10}$  found with man in fever and with the curarized dog, the protoplasm of warm-blooded and cold-blooded animals are basically alike. But it should not be forgotten that the  $Q_{10}$  of 2 or 3 is also an expression of the rate of practically all chemical reactions. For instance, one might possibly compare the reaction to temperature of the protoplasm of the snake with the reaction of a mixture of potassium hydrate and sulphuric acid in a test tube. The reaction would be doubled or trebled with each

<sup>1</sup> Krogh, A., *Internat. Zeitschr. f. physik.-chem. Biol.*, 1914, **1**, p. 507.

<sup>2</sup> Du Bois, E. F., *Basal Metabolism in Health and Disease*, Philadelphia, 2d ed., 1927, pp. 389 and 390.

<sup>3</sup> Giaja, J., *Ann. de Physiol.*, 1925, **1**, p. 596.

10-degree increase in temperature in both instances. Hence in view of the general uniformity of the  $Q_{10}$  for all chemical processes, the fact that all cold-blooded animals, man in fever, and the curarized dog have a  $Q_{10}$  of the same magnitude loses special significance biologically, except in so far as biological processes are chemical processes.

The  $Q_{10}$  for the hibernating marmots of Mareš can not be computed, since he measured the metabolism of his marmots while hibernating at about 10° only and not at a number of different temperatures. Nagai measured his hibernating marmots at 13.5° and 24.4°, as well as at 10°. According to Nagai's measurements, we have computed that the  $Q_{10}$  for the hibernating animal is apparently of a much higher order than that found with cold-blooded animals, for based upon his oxygen curve the  $Q_{10}$  between 10° and 20° would be 6.0 and upon his carbon-dioxide curve, 7.0 (fig. 106, p. 483). These values indicate a more intense reaction on the part of the hibernating animal to environmental temperature than is found not only with our cold-blooded animals but with chemical reactions and biological processes under normal conditions. Undoubtedly the higher  $Q_{10}$  represents the special conditions when the marmot's metabolism is accelerated due to the awakening from winter sleep. The practical value of the  $Q_{10}$  is well brought out by our efforts to compute the metabolism of Mareš' marmots at 16° from the values obtained at 10°, using the  $Q_{10}$  computed from the measurements of Nagai (page 489).

## METHODS OF PREDICTING METABOLISM OF COLD-BLOODED AND WARM-BLOODED ANIMALS AT TEMPERATURES ABOVE AND BELOW THOSE STUDIED

Emphasis has been laid in the comparisons in the immediately foregoing pages upon the influence of an increasing environmental temperature upon the rate of the metabolic reaction. It is likewise of importance to compare the actual *level* of the heat production of cold-blooded and warm-blooded animals at different body temperatures. Since an unusually large number of our measurements on cold-blooded animals were made at or near 16°, 22° and 30°, these particular temperature levels have been selected for the comparisons and, because the cell temperature of most warm-blooded animals is 37°, this temperature has likewise been chosen. Some of our cold-blooded animals were studied over a wide range of temperature and at fairly frequent points. Others, notably the giant tortoises, the lizards and the alligator, were studied only over a short range, owing to the practical difficulties of replacing them in case they were accidentally overheated. In the final analysis of our data it is desirable to attempt some estimate for these animals that were measured only over a short temperature interval, as to their probable metabolism at temperatures above and below those at which they were actually studied. Specifically, many cold-blooded animals have been measured by other investigators at 16°. Not all our animals were measured at as low a temperature as this. Is it



possible to predict from the observations available the probable metabolism of our animals at this low temperature level? Again only a few of our animals were measured at a temperature as high as  $37^{\circ}$ . There is a general impression that cold-blooded animals do not withstand having their cell temperature raised to  $37^{\circ}$ , that they are actually damaged and subsequently reflect in their metabolism an injured protoplasm. Is it possible to predict from the observations secured over the temperature range studied what would be the probable metabolism of these animals at  $37^{\circ}$ ? Finally, it will be desirable to compare the metabolism of hibernating animals with that of our cold-blooded animals. The observations upon hibernating animals that inspire one with the greatest confidence are those obtained by Mareš<sup>1</sup> on the marmot and those by Nagai,<sup>2</sup> also on the marmot. The latter have been cited in some detail by Rubner.<sup>3</sup> Both these series of measurements, however, were carried out at a much lower temperature than any that prevailed in our experiments. Thus Nagai's marmots were measured in deep sleep at a body temperature of  $10^{\circ}$  and again when awake at  $37^{\circ}$ . Mareš measured his animals while hibernating at external temperatures varying from  $4^{\circ}$  to  $11.8^{\circ}$ , and averaging  $8.4^{\circ}$ . The rectal temperature is not given, but it has been assumed that the probable average rectal temperature was  $10^{\circ}$ . His animals were measured again when awake at a rectal temperature of  $37^{\circ}$  (environmental temperatures varying from  $6.7^{\circ}$  to  $21.0^{\circ}$ ). One especially uniform experiment of Mareš, extending over three days, was made at an average environmental temperature of  $4.3^{\circ}$  (probable rectal temperature  $5^{\circ}$ ). It is highly important to predict, if possible, what would have been the metabolism of these marmots had they been measured, for example, at  $16^{\circ}$ , for purposes of comparison not only with our own observations but with those of other writers.

Several methods of comparing the metabolism of animals at temperatures above and below the temperature range within which they have been studied are available. One is to calculate from the measured metabolism at a given temperature the metabolism at the desired higher or lower temperature, by applying the value for the *percentage* increase or decrease found to obtain within the temperature range studied (see pages 438 to 439). This calculation has been frequently carried out and is reasonably accurate when the temperature interval represented by the prediction is not too great, that is, not over  $8^{\circ}$  or  $10^{\circ}$ . When it is much greater than 10 degrees, the prediction of the metabolism at any intervening temperature on the basis of the percentage change in metabolism at the two studied temperatures is liable to great error. Furthermore, such a calculation assumes that the increment in metabolism with increasing temperature is a straight-line relationship, and it is clear from all our curves, except those for tortoises, that the relationship between metabolism and temperature with cold-blooded animals is not a straight-line function.<sup>4</sup> A second method

<sup>1</sup> Mareš, F., *loc. cit.*

<sup>2</sup> Nagai, H., *Zeitschr. f. allg. Physiol.*, 1909, **9**, p. 243.

<sup>3</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 303.

<sup>4</sup> This has likewise been strikingly shown by A. Krogh, *The Respiratory Exchange of Animals and Man*, London, 1916, fig. 28, p. 96.

is to calculate the probable metabolism from the measured metabolism and the  $Q_{10}$  found to obtain at the 10-degree temperature interval nearest the temperature at which one wishes to predict the metabolism. But here again the same criticisms that apply to the use of the percentage factor apply to the use of the  $Q_{10}$  factor, that is, the accuracy of the prediction by means of the  $Q_{10}$  factor depends upon the extent of the temperature interval and whether the relationship between the metabolism and the temperature is a straight-line relationship.

A third method of predicting the metabolism of an animal at a temperature above or below the actually measured range is what might be called the method of inspection. From the several curves that have been sketched for our different cold-blooded animals, the general trend of the metabolism with increasing temperature is fairly clearly indicated.<sup>1</sup> It is not the same for all the different species and yet nearly so, save for the tortoises. It is, therefore, conceivable that in the case of a metabolism curve that does not extend beyond 30°, for example, by simply projecting the curve to 37° according to one's own judgment as to what the probable trend of the curve would be (based upon inspection of the trend already indicated), one could predict the metabolism at the higher temperature without introducing an error at all commensurate with the error involved in the application of a percentage factor or a  $Q_{10}$  factor, which would imply a straight-line relationship. Mathematically, it is conceivable that the metabolism at a desired high temperature could be predicted by applying the  $Q_{10}$  factor obtained for the last 10-degree temperature interval over which the animal was measured to the metabolism value secured at the temperature studied nearest to that of the desired temperature. Practically, the inaccuracies in this type of prediction or in the prediction by the use of the percentage factor are so great that in all probability the method of inspection will yield results more strictly in accordance with the truth. Hence, although the factors for the  $Q_{10}$  and the percentage decrease or increase in metabolism have been discussed in the preceding pages as evidence of the uniformity in the rate of reaction of the metabolism of cold-blooded animals to changing temperatures, the method of inspection will be used to predict the metabolism at temperatures outside the measured range, whenever possible, and no use will be made of either the  $Q_{10}$  or the percentage factors except in those few instances when the method of inspection from a curve is not available. The method of inspection is especially justified by the frequent, short temperature intervals at which our measurements were made. Therefore no calculations based upon long temperature intervals are needed.

<sup>1</sup>It is becoming an increasing custom, especially with those biometrists who are particularly interested in physiology, to employ logarithmic plots. In the mathematical treatment of this rather difficult method of prediction, the possibility was considered of plotting our data logarithmically or semi-logarithmically. Indeed, all the various snake curves were plotted on the semi-logarithmic basis. But these logarithmic plots did not alter sufficiently the general picture shown by the charts presented in the preceding pages to justify reproducing them in this already too large report.

## COMPARISON OF STANDARD METABOLISM OF COLD-BLOODED ANIMALS AT DEFINITE BODY TEMPERATURES

### STANDARD METABOLISM OF COLD BLOODED ANIMALS IN NUTRITION LABORATORY SERIES AT 16° AND 30° C.

The most extensive recent consideration of the metabolism of cold-blooded animals is that contained in the two reports published by Rubner in 1924.<sup>1</sup> Doubtless influenced considerably by the fact that his classic study on warm-blooded animals had been carried out at 16° and comparisons made at this temperature, Rubner has preferred to make his comparisons of cold-blooded animals also on the basis of 16° C. For reasons set forth elsewhere in this report (pp. 496 to 501) we believe that 30°, at least with the animals we studied, represents more nearly the optimum temperature or the normal living conditions for these animals. It is generally believed that cold-blooded animals do not readily withstand heating to 37°, save under special conditions of lowered humidity, and it has already been shown in the analysis of the respiratory quotients of our 1931 python (p. 411) that the cold-blooded animal, particularly the snake, may have a special qualitative metabolism at a temperature even as high as 18°. Hence to study the cold-blooded animal at 16° may be as abnormal as to study it at 37°. Nevertheless, since Rubner's comparisons were made at 16° and since many of our cold-blooded animals were studied at or near 16° and 30°, the values for the average standard metabolism at these two temperatures, both per kilogram of body weight and per square meter of body surface, have been drawn from the various smoothed curves shown in the preceding charts and have been summarized for comparison purposes in table 116. This tabular analysis is, in a way, an elaboration of the comparisons made earlier in this report of the curves in figures 99 and 100 (pp. 426 and 428). In a number of instances the metabolism measurements were not made at exactly 16°. Thus, the lowest temperature with the alligator was 19.5° and with the tortoises 17.2°. It seems best in these instances to record the values at the temperatures actually studied, rather than to project the curves by inspection to predict the metabolism at 16°. Hence the data for these particular animals can not be directly compared with the data for the other animals without this reservation in mind.

In discussing the variability in the metabolism of these different species of cold-blooded animals, we shall compare the maximum with the minimum heat value at each temperature and compute the percentage difference based upon the minimum value. Strictly speaking, the percentage difference should be calculated to show the *average* deviation above and below the *average* metabolism for all the groups. In this particular comparison, however, we wish to determine what is the greatest possible difference between the various groups of animals rather than to note how closely the groups agree with each other. Obviously this method of computing the variability makes the percentage difference greater than it would be if based upon the average for all the groups.

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, pp. 222 and 268.

The range in the heat production per kilogram of body weight per 24 hours at 16° is from 0.55 calorie with the boas to 1.14 calories with the gopher snakes, that is, there is a difference of slightly over 100 per cent of the minimum value. The alligator had a heat production of 0.85 calorie at 19.5°, which, if projected to 16°, might be not far from 0.6 or 0.7 calorie. However, since its metabolism was measured at only two temperatures, 19.5° and 22.1°, it does not seem justifiable to attempt to predict what its heat production would be at 16°. If a general average value were permissible for the four groups of snakes, it would be 0.79 calorie. The values for the heat production per square meter of body surface at 16° are reasonably uniform for the four groups of snakes, averaging 10.9 calories.

TABLE 116—*Comparison of standard metabolism of the cold-blooded animals in the Nutrition Laboratory series at 16°, 30° and 22° C.*

Animal	16°		30°		22°	
	Heat produced per 24 hours					
	Per kg.	Per sq. m.	Per kg.	Per sq. m.	Per kg.	Per sq. m.
	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>	<i>cal.</i>
Pythons. . . . .	0.70	13.0	3.00	46.0	1.38	22.5
Boas. . . . .	.55	9.8	2.70	47.0	1.13	21.2
Rattlesnakes. . . . .	.77	9.6	4.00	52.8	1.85	24.5
Gopher snakes. . . . .	1.14	11.0	5.30	58.0	2.24	22.5
Lizards. . . . .			5.85	59.0	<sup>12</sup> 2.50	<sup>12</sup> 28.0
Tortoises (5-kg.) <sup>2</sup> . . . . .	<sup>3</sup> 1.00	<sup>3</sup> 17.0	5.18	73.2	2.48	37.7
Tortoises (giant) <sup>2</sup> . . . . .					2.48	85.0
Alligator (53-kg.) <sup>4</sup> . . . . .	<sup>4</sup> .85	<sup>4</sup> 25.4			1.00	29.9

<sup>1</sup> Assumed from inspection of trends of curves in figures 99 and 100, pages 426 and 428.

<sup>2</sup> Calculations based on flesh weight.

<sup>3</sup> At 17.2° C.

<sup>4</sup> At 19.5° C.

The alligator's heat production on this basis was 25.4 calories at 19.5°. If a correction were permissible to predict its metabolism at 16°, it is unlikely that the reduction would be great enough to bring the heat production down to 11 calories, the average for the snakes. The tortoises evidently are in a class by themselves on the body-surface basis, undoubtedly in part at least because of the uncertainty in the calculation of the weight of shell and the body surface.

It has been possible to include the lizards among the animals studied at 30°. The metabolism per unit of body weight at 30° (as at 16°) varies greatly, from 2.70 calories with the boas to 5.85 calories with the lizards, that is, a difference between the minimum and maximum values of 115 per cent. Per unit of body surface the metabolism at 30° shows more nearly the same uniformity among all the various groups of animals as was noted on this basis with the four groups of snakes at 16°, that is, it varies only from 46.0 to 73.2 calories, and the difference between these two values is only 59 per cent of the minimum value. It should be borne in mind, however, that the giant tortoises, with which the greatest differences could

be expected, are not included in the values per unit of body weight and per unit of surface area reported in table 116 at 16° and at 30°, because they were not measured at 16° and 30° and because their data on the body-surface basis deviate too widely from the data for the 5-kg. tortoises (fig. 98, p. 398) to justify including them in any general curve.

The comparison of the data for snakes and lizards, that is, not including the values for the alligator and the tortoises in table 116, shows that the metabolism at 16° and at 30° is more uniform on the body-surface basis than on the body-weight basis. If the alligator and the tortoises are not taken into consideration, however, the picture is imperfect and hence unsatisfactory. It may be assumed that these animals would have a somewhat lower metabolism at 16°, both per kilogram of body weight and per square meter of body surface, than that recorded in table 116. But even with this assumption, the extremes in the heat production per kilogram of body weight are still found with the boas and the gopher snakes, and the inclusion of the tortoises and the alligator does not affect the picture on this basis of comparison at 16°. On the body-surface basis the highest values at 16° recorded in table 116 are for the tortoises and the alligator. These would undoubtedly be lowered if corrected to 16°. It is possible that the value for the alligator might be reduced from 25.4 to 18 calories. Even then it would still be twice as great as the value for the rattlesnakes, that is, there would be a difference of 100 per cent between the two values. But the range in values for the heat production per kilogram of body weight at 16° is from 0.55 calorie with the boas to 1.14 calories with the gopher snakes, or a difference of 100 per cent. Hence at this particular temperature level, 16°, the comparison among *all* the animals is in favor of the heat production per square meter of body surface. At 30° the difference in the extremes in heat production per kilogram of body weight (from 2.70 to 5.85 calories) when all the animals are considered is much greater percentagewise than that on the body-surface basis (from 46.0 calories with the pythons to 73.2 calories with the tortoises). At 30°, therefore, as well as at 16°, the comparison among all the animals is to the advantage of the expression per unit of surface area. It must again be emphasized, however, that at 30° there are no measurements on the alligator and that the giant tortoises are not included in either comparison at 16° or 30°, for they were all measured only at or near 22° C.

#### STANDARD METABOLISM OF COLD-BLOODED ANIMALS IN NUTRITION LABORATORY SERIES AT 22° C.

Table 116 was prepared primarily to compare animals at 16°, the temperature selected by Rubner for his comparisons, and at 30°, the temperature more frequently employed in the Nutrition Laboratory experiments. There are certain disadvantages in making the comparisons at these two temperatures in that none of our giant tortoises were measured at 16° or 30°. They were measured more nearly at 22°. Hence table 116 includes likewise the values drawn from the various smoothed curves for the metabolism of the different species of animals at 22°, in order to introduce the values for the giant tortoises. In all instances except the lizards the

metabolism was actually measured at this temperature. In the case of the lizards the curve has been projected by inspection from the 25-degree level to 22°, in order to obtain values for comparison with the results for the other animals. With the tortoises the standard heat production per kilogram of flesh weight both of the giant and of the 5-kg. tortoises averages the same, namely, 2.48 calories at 22°. Per unit of surface area the metabolism is not the same for both groups. On the basis of the metabolism per kilogram of body weight, the values at 22° range from 1.00 calorie with the alligator to 2.50 calories with the lizards, a difference of 150 per cent of the minimum. On the basis of the metabolism per unit of surface area the values, not including that for the giant tortoises, deviate less widely, that is, from 21.2 calories with the boas to 37.7 calories with the 5-kg. tortoises, a difference amounting to 78 per cent of the minimum.

If from figure 100 (p. 428) one makes a crude estimate as to the average metabolism of the giant tortoises, it would be about 85 calories per square meter of body surface at 22° C. To average this value directly with the value of 37.7 calories for the 5-kg. tortoises given in table 116 is admittedly debatable. If, for purposes of discussion, one used an average value of 60 calories at 22° to represent the two groups of tortoises, both large and small, the variability in the metabolism at 22° on the body-surface basis would be nearly threefold, ranging from 21.2 calories with the boas to 60 calories with all the tortoises. Since on the basis of the heat production per kilogram of body weight the range among all the animals is still from 1.0 calorie with the alligator to 2.50 calories with the lizards, the variability is 250 per cent. When all the animals are considered, therefore, there is a slight advantage in favor of the comparison per kilogram of body weight. When all the groups of animals except the giant tortoises are considered, the computation of the metabolism per unit of body surface appears on the whole the better method of the two for comparing animals of different sizes and species. When the giant tortoises are included (and there is no good reason for excluding them), the picture is reversed. Had our study dealt only with 5-kg. tortoises, the picture would have been extraordinarily clear and definite. If no other justification for the use of the giant tortoises existed than to point out this striking difference in the two bases of comparison, the experiments would have been well worth while.

The results for the large and the small snakes agree better on the body-surface basis than on the body-weight basis. But the comparison of the metabolism of the giant tortoises with that of the 5-kg. tortoises, although showing fairly uniform results when the heat production is computed per unit of flesh weight, gives more divergent results when the metabolism is referred to surface area. To be sure, the surface area was not actually measured but computed from the two-thirds power of the flesh weight (itself a computed factor) times a constant, the accepted method at the present day.

The low value of 1.00 calorie per kilogram of body weight found with the alligator at 22° raises the point as to whether the size of this animal (53 kg.) may not have accounted for its low metabolism. In general, with warm-blooded animals the thesis that the larger animal has the smaller

heat production per kilogram of body weight is well established. The largest of our other cold-blooded animals were the three giant tortoises, weighing 69, 80 and 132 kg., respectively. Their metabolism per kilogram of flesh weight was found to agree closely enough with the metabolism of the 5-kg. tortoises to permit the sketching of a curve to represent the general trend of the metabolism of all the tortoises. Thus, at 22° their average metabolism may be said to be about 2.50 calories per kilogram of body weight, or 150 per cent greater than that of the 53-kg. alligator, notwithstanding their larger size. Among the snakes the largest animal was the 32-kg. python. According to the average curve for all pythons (see fig. 48, p. 214) the probable heat production per unit of weight of this species of snake at 22° would be 1.38 calories. Reference to table 54 shows that, although the metabolism of the 32-kg. python was not measured exactly at 22°, it was studied at 21.5° and the result lies close to the curve representing the general trend of the metabolism of this particular animal. According to the general curve for this large python (fig. 46, p. 206), its metabolism at 22° would be 1.25 calories per kilogram of body weight, or only 25 per cent greater than that of the 53-kg. alligator. The relatively small boas, on the other hand, have on the average a metabolism at 22° of 1.13 calories, that is, closely approximating that of the alligator. It would appear, therefore, that this alligator does not have a specifically low metabolism because of its size. The relatively low metabolism of the 32-kg. python per unit of body weight, when compared with that of the other groups of animals, might be explained by the fact that this python was studied only after it had been fasting for a considerable length of time, between 184 and 221 days, and the prolonged fast would tend to result in a low rather than a high metabolism. The low value for the alligator, however, can not be explained by prolonged fasting, for as a rule alligators are good feeders and this particular alligator had probably not fasted more than three days.

In any consideration of animals of different sizes, particularly where the differences in size are large, the common method for comparison is on the basis of the heat production per square meter of body surface. When the results per unit of surface area are considered, it can be seen that the 53-kg. alligator had a heat production at 22° of 29.9 calories, this being a little, although insignificantly, higher than that of the other animals, save the tortoises. It is only 1.9 calories higher than the 28 calories for the lizards, which weighed about 1 kg. Thus in this particular comparison, size is without significance. That the value of 37.7 calories for the 5-kg. tortoises, whose flesh weight averaged about 3.0 or 3.5 kg., is measurably above that of the 53-kg. alligator speaks for a higher metabolism in the smaller animal, but in consideration of the comparison of the 53-kg. alligator and the 1-kg. lizards this must be interpreted as an indication solely of the specifically high metabolism of the tortoises, irrespective of size. If, for the moment, one considers that the giant tortoises have a heat production per unit of surface area of 85 calories (the uncertainty in establishing this value is recognized), it can be seen that both per kilogram of body weight and per unit of surface area the alli-

gator, which was smaller than the giant tortoises, has a lower metabolism. So far as this particular comparison is concerned, the influence of size would be in the nature of a lower metabolism with the smaller animals. Comparison of the value of 1.00 calorie per kilogram of body weight for the alligator at 22° and that of 2.48 calories for the tortoises, a value which includes the giant tortoises as well as the 5-kg. tortoises, speaks again for the specifically high metabolism of the tortoises, especially when the great weight of the giant tortoises is taken into consideration.

The specifically high metabolism of the tortoises can not be ascribed to the after-effect of digestion, for, although in some instances the tortoises had been only 24 hours without food, in most instances they had been fasting for a much longer period extending over several days. In any event, the effect of any previously ingested food must have been immediate and can hardly account for the great differences noted between the metabolism of the tortoises and that of the other cold-blooded animals. Evidently the irritability of the tortoise protoplasm is of a different order from that of the python, for example. The tremendous muscular strength of the tortoise (exemplified by the fact that the 132-kg. tortoise could easily carry a man around on its back), although exercised very deliberately and by no means continuously, may be comparable to the constricting strength of a large python. But for the most part the tortoise is cumbersome, sluggish, and inactive for a large part of the time and, although capable of great muscular effort, the actual time during which such effort is indulged in is short. Hence the energy needs for muscular work throughout the day are small. The tortoise is incapable of quick, lightning-like movements, such as the snake occasionally makes. Many of the lizards and the alligators, on the other hand, are likewise capable of rapid movements. It is a question whether the difference between the purely vegetarian diet of the tortoise and the insectivorous or animal diet of most of the other animals in our series could explain the difference in the metabolic levels. The large Galapagos tortoises apparently subsist upon an exclusively vegetarian diet, in large part cacti. A study of great interest would be the determination of the nitrogen metabolism of these large animals over a considerable period of time, to compare with the supposedly high nitrogen metabolism of the snake.

#### COMPARISON OF STANDARD METABOLISM OF COLD-BLOODED ANIMALS IN NUTRITION LABORATORY SERIES WITH THAT OF COLD-BLOODED ANIMALS MEASURED BY OTHERS AT OR NEAR 16° C.

A comparison between the various cold-blooded animals studied in the Nutrition Laboratory research has been made in different sections of this report, but it is important now to compare the findings on our cold-blooded animals with those of other writers, in so far as the actual level of the metabolism at definite body temperatures is concerned. This comparison will involve differences in technique and in some cases will consider investigations carried out many years ago, but perhaps the greatest criticism against the comparison will be the uncertainty with regard to the activity



of the animals, on the basis of the general belief that small animals are inclined to be somewhat more active than large animals. The Nutrition Laboratory research was confined almost exclusively to large animals, and the observations of other investigators were for the most part with small animals. It becomes necessary, therefore, in any comparison of the earlier data with the Nutrition Laboratory series to employ the two methods (already discussed) of comparing the metabolism of animals of greatly different size, one being the computation of the heat production per kilogram of body weight and the other that per square meter of surface area. It has been proved that with warm-blooded animals of the same or different species, under conditions in which the factor of activity can for the most part be ruled out, the smaller the animal the larger the heat production per kilogram. It is commonly accepted that with warm-blooded animals there is no difference in the heat production per square meter of surface area, whether the animal is large or small. In this view the Nutrition Laboratory does not concur.

Our cold-blooded animals were studied at a number of temperatures over a considerable range, and thus representative curves could be drawn through the plotted data to indicate the general trend of the metabolism with increasing temperature. Most of the earlier investigations were confined to measurements at only one, two, or at the most three temperatures. Hence curves can not usually be drawn for the earlier data. The notable exception to this is the excellent series on small cold-blooded animals by Krogh. The comparison, therefore, of the Nutrition Laboratory data with the earlier results seems best made, not by attempting to obtain fictitious curves from the earlier values, but by considering the actual values determined as nearly as possible at one or two definite temperatures. It so happens that many measurements have been made at or close to 16°. Furthermore, this particular temperature has been used extensively in the calculations of Rubner, who has corrected earlier observations at somewhat different temperatures in order to estimate the probable metabolism at 16°. Another temperature at which many of our own animals and a number of others have been measured is 30°. For the time being, the discussion will be confined to comparisons at these two temperatures, although subsequently the metabolism of cold-blooded animals when raised to the temperature of the average warm-blooded animal, 37°, will be considered (see pages 494 to 506).

At the lower temperature a considerable series of measurements have been made, either exactly at or within a few degrees of 16°. These results have been incorporated in table 117, arranged for the most part in the order of increasing body weights, beginning with the 2.5-gram stickleback of Rubner and ending with the 53-kg. alligator of the Nutrition Laboratory series, and in most instances corrected to 16°, if not actually determined at that temperature. The giant tortoises used by the Nutrition Laboratory were not measured at as low a temperature as 16°, and hence are not included in this table. The values of other investigators for the heat production per kilogram of body weight have been obtained from the publications cited in the footnotes in table 117. The calculation of these values

requires no particular discussion. The values per square meter of body surface, however, need special emphasis in that the constant for computing the surface area of the frog, originally used as 4.62, has been shown to be wrong, and in the calculations reported in this table a constant of 10 has been employed. This applies likewise to the calculations for the

TABLE 117—*Comparison of metabolism of cold-blooded animals of different species at or near 16° C.*

Animal	Body weight	Heat produced per 24 hours		Investigator
		Per kg. <sup>1</sup>	Per sq. m. <sup>1</sup>	
		<i>cal.</i>	<i>cal.</i>	
Stickleback.....	2.5 gm.	29.4	42.4	Rubner. <sup>2</sup>
Goldfish.....	4.0 gm.	12.0	22.4	Rubner. <sup>2</sup>
Goldfish.....	9.3 gm.	8.2 +	19.0 +	Krogh. <sup>3</sup>
Lizard.....	21.0 gm.	5.3 +	11.6 +	Regnault and Reiset <sup>4, 2</sup> .
Frog (normal).....	46 to 50 gm.	12.8	46.2	Rubner. <sup>2</sup>
Frog (narcotized).....	30.0 gm.	6.5	19.0	Krogh. <sup>3</sup>
Toad (decerebrated).....	34.3 gm.	2.5	7.5	Krogh. <sup>3</sup>
Frog (curarized).....	35.0 gm.	5.2	17.0	Krogh. <sup>3</sup>
Frog (normal).....	35.0 gm.	5.8	17.5	Krogh. <sup>3</sup>
Tortoise.....	<sup>5</sup> 135.0 gm.	6.5	33.0	Rubner. <sup>2</sup>
Lizard.....	110.0 gm.	12.0	46.0	Krehl and Soetbeer <sup>6, 2</sup> .
Lizard.....	374.0 gm.	4.2	30.0 +	Martin. <sup>7</sup>
Frog.....	600.0 gm.	7.5	64.0	Krehl and Soetbeer <sup>6, 2</sup> .
Alligator.....	1380.0 gm.	5.0	47.0	Krehl and Soetbeer <sup>6, 2</sup> .
Uromastix.....	1250.0 gm.	4.5	29.0	Krehl and Soetbeer <sup>6, 2</sup> .
Tortoise.....	<sup>3</sup> 3 to 4 kg.	1.00 -	17.0 -	Nutrition Laboratory.
Gopher snake.....	2 kg.	1.14	11.0	Nutrition Laboratory.
Rattlesnake.....	2 to 5 kg.	.77	9.6	Nutrition Laboratory.
Boa.....	7 to 8 kg.	.55	9.8	Nutrition Laboratory.
Python.....	15 kg.	.70	13.0	Nutrition Laboratory.
Alligator.....	53 kg.	.85 -	25.4 -	Nutrition Laboratory.

<sup>1</sup> Most of these values were actually determined at or "corrected to" 16°. A few were obtained at temperatures one or two degrees above or below 16°. Rather than recompute them with an assumed temperature coefficient, we have indicated by a plus sign when the correction would raise the value, and by a minus sign when it would lower it.

<sup>2</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, pp. 222 and 268.

<sup>3</sup> Krogh, A., *Internat. Zeitschr. f. physik.-chem. Biol.*, 1914, **1**, p. 491; Ege, R., and A. Krogh, *Internat. Revue f. Hydrobiol.*, 1914, **6**, p. 48.

<sup>4</sup> Regnault, V., and J. Reiset, *Annales de Chim. et de Phys.*, 1849, 3d ser., **26**, p. 299.

<sup>5</sup> Flesh weight.

<sup>6</sup> Krehl, L., and F. Soetbeer, *Arch f. d. ges. Physiol.*, 1899, **77**, p. 611.

<sup>7</sup> Martin, C. J., *Philos. Trans., B*, 1903, **195**, p. 1.

tortoises, both that of Rubner and those of the Nutrition Laboratory series. The body-surface constants employed for the other animals have not been altered. For the Nutrition Laboratory series it has been necessary to report the *average* weight of each *species* of animal. This, however, in the case of the tortoises is not far from the weight (flesh) of each individual animal. Among the rattlesnakes, some individuals weighed twice as much as others. The average weight of the boas was about 7 or 8 kg., but varied from 4 to 12 kg. The pythons averaged 15 kg., although

one weighed 32 kg. and two others about 6 kg. each. Only one alligator was studied, weighing 53 kg.

The importance of including the actual weights of the animals in table 117 will soon be apparent, for an inspection of the values for the heat production per kilogram of body weight shows that there is a general, although by no means regular, tendency for the heat production per unit of weight to be somewhat lower, the larger the body weight. This is notably the case in the Nutrition Laboratory series as a whole. Indeed, the Nutrition Laboratory values are much lower than any of the other values, the lowest value in the table except for our own series being that of 2.5 calories for the decerebrated toad of Krogh. All our animals have a metabolism at 16° of 1.14 calories per kilogram of body weight or below. That this is not exclusively a feature of the body weight is apparent from our previous considerations. Thus, of two groups of boas, one weighing 4 kg. and the other 12 kg., the 4-kg. boas, at temperatures between 27° and 29° C., produced on the average 3 calories per kilogram of body weight and the 12-kg. boas 2 calories. That is, the smaller boas, like warm-blooded animals, had the larger heat production per unit of weight (fig. 61, p. 233). Offsetting this finding is the fact that the giant python, weighing 32 kg., had the largest heat production per kilogram of body weight of any of the pythons. The only animals studied by the earlier investigators that approximate in weight our smallest animals are the alligator and the *Uromastix* of Krehl and Soetbeer. These weighed 1.38 and 1.25 kg., respectively. Their heat production per kilogram of body weight was, however, four times that of our 2- to 3-kg. animals, such as the gopher snakes and the tortoises (flesh weight). It is conceivable that the animals in the Nutrition Laboratory series were on the whole quieter than those in the earlier series. Certainly if one compares the results for the alligator and the *Uromastix* of Krehl and Soetbeer, weighing 1.38 and 1.25 kg., respectively, with the values for Krogh's frogs of 35 grams, for the lizards of Regnault and Reiset of 21 grams, and for Martin's lizards of 374 grams, there is not a striking difference in the heat production per kilogram of body weight, although there are great differences in the weights of the animals. On the other hand, there is nothing approximating uniformity in the metabolism per unit of weight either among the animals in the earlier series or in the Nutrition Laboratory series, for in our own series the values range from 0.55 calorie with the boas to 1.14 calories with the gopher snakes.

Although, as Rubner has pointed out, one may not compare different species<sup>1</sup> of cold-blooded animals on the basis of the heat production per square meter of body surface, the calculation of the metabolism per unit of surface area for animals of the same species is not only permissible but gives more closely comparable results than does the calculation per unit of weight. In the consideration of the values in table 117 for the heat production per square meter of surface area, therefore, one must confine the comparisons to fish alone, or frogs, lizards, tortoises, alligators, or snakes alone. The heat production per unit of surface area at 16° ranges from

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 285.

19+ calories with the goldfish of Krogh to 42.4 calories with the small stickleback of Rubner. Among the lizards, the values range from 11.6+ calories with the 21-gram animals of Regnault and Reiset to 46 calories with the 110-gram lizard of Krehl and Soetbeer. Among the frogs and toads the variability is striking, the values ranging from 7.5 calories with the decerebrated toad of Krogh to 64 calories with the giant frog of Krehl and Soetbeer. For the tortoises there exist in the earlier literature only the observations of Rubner that lend themselves to correction to 16°. We have computed that Rubner's tortoise at 16° (using a body-surface constant of 10) would have produced 33 calories per square meter of body surface as compared with the 17- calories found for the Nutrition Laboratory tortoises. The 1380-gram alligator of Krehl and Soetbeer and the 53-kg. alligator of the Nutrition Laboratory series had a heat production of 47 and 25 calories, respectively. The snakes are represented only by the Nutrition Laboratory series. Their heat values range from 9.6 to 13.0 calories per square meter of body surface.

In view of the fact that the data in table 117 were secured by different observers, with different techniques, and with frequently a long period of time between the observations, it is not surprising that the closest agreement between different species is found in the Nutrition Laboratory series of snakes. Perhaps the most striking feature, however, in connection with the table is the fact that the Nutrition Laboratory values on the body-surface basis, with the single exception of the value of 25 calories for the alligator, are markedly lower than all the other observations save those for the decerebrated toad of Krogh and the lizard of Regnault and Reiset. This is in line with the finding that the heat production per kilogram of body weight is lowest in the Nutrition Laboratory series, but it has already been pointed out that these low values on the body-weight basis may be explained solely by the fact that this particular series represented the largest animals. In the earlier discussions in this report it has been shown that in the Nutrition Laboratory series (leaving out the giant tortoises, which do not figure in this particular comparison) the metabolism of the various groups of animals studied is more uniform per square meter of body surface than per kilogram of body weight. It has been argued by earlier writers that Rubner's surface-area law is equally applicable to cold-blooded animals,<sup>1</sup> although this has been disavowed strongly by Rubner himself. Rubner has calculated that the heat production per square meter of body surface for fish ranging from 0.5 gram to 245 grams is 33 calories per 24 hours at 16°. To compare with this he reports the calculated heat production per square meter of body surface per 24 hours of the animals of Krehl and Soetbeer, his own tortoise, and a collection of frogs and toads. If these values are corrected so that, instead of using 4.6 for the surface-area constant the more correct factor of 10 is employed, the results for frogs and toads and tortoises will be reduced a little more than one-half, and the average value for his six groups of amphibians and reptiles will be 44 calories per square meter of body surface per 24 hours rather than 68.5 calories. This corrected value

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 241.

of 44 calories compares well with the 33 calories found with his fish, but is measurably above the results for the Nutrition Laboratory series. If a general average were permitted for the Nutrition Laboratory series of animals measured at or near  $16^{\circ}$ , it would be about 14 calories per square meter of body surface or only about one-third of the corrected average for Rubner's series of amphibians and reptiles. According to the revised calculation of Rubner's data, the heat production per square meter of surface area is practically as uniform among different species of amphibians and reptiles as it is among different sizes of fish. Thus, with the fish the values range from 26 to 44 calories and with the amphibians from 29 to 64 calories or, if the frogs are not considered, from 29 to 47 calories. If the metabolism of these same animals is computed per kilogram of body weight, as has been done in table 117, it can be seen that the values on this basis vary much more than on the body-surface basis. Rubner's contention that the heat production per unit of surface area among different animals of the same species is much more regular than that per unit of body weight is definitely shown in his values for fish. When, in addition, the revised calculations for the heat production per square meter of body surface of different amphibians and reptiles are compared not only with each other but with the values for the fish, this comparison again speaks for the general applicability of the surface area law. At least there is a much closer agreement in the values than when the calculations are made upon the body-weight basis. The animals in this particular comparison did not exceed 1.4 kg. in weight. Since with the Nutrition Laboratory groups of animals also, which weighed much more, the variability in the metabolism at  $16^{\circ}$  has been found to be much less on the surface-area than on the weight basis, this finding, as far as it goes, speaks strongly for the applicability of the surface-area law not only among animals of the same species but among different cold-blooded animals of different species, even to the extent of comparing the amphibians and reptiles with the fish.

This discussion has to deal exclusively with the measurements and computations of the metabolism at  $16^{\circ}$ , the temperature selected by Rubner for his most extensive comparisons. Had the giant tortoises been measured at  $16^{\circ}$  (and they were not measured except at  $22^{\circ}$ ), it is highly probable that the picture would have been considerably altered, in that unusually high values would have been found per square meter of body surface for the giant tortoises, whereas values more like those for the other groups of animals would have been found per kilogram of flesh weight. If, therefore, the probable computed metabolism of the giant tortoises at  $16^{\circ}$  is included in the comparison, this one aberrant group of animals speaks against the general applicability of the surface-area law to cold-blooded animals or else raises the question as to whether the body surface of the tortoise has been calculated correctly. This method of calculation, with all its obvious possibilities of error (see pp. 355 to 365) remains at present our only means of even approximating the surface area of these animals.

The *average* heat production per unit of surface area per 24 hours at  $16^{\circ}$  is 33 calories for Rubner's group of fish, 44 calories for the six groups of

amphibians and reptiles cited by Rubner, and 14 calories for the entire Nutrition Laboratory series. This latter value is somewhat less than half of the average value for Rubner's fish and one-third of his corrected average value for reptiles and amphibians. The difference in these average results, in spite of the agreement of the individual values in the different series, can be explained on two possible grounds, the precaution of the Nutrition Laboratory to rule out periods of muscular activity (exemplified by the fact that graphic records of the degree of repose accompanied every experiment) and the fact that the Nutrition Laboratory series as a whole represents large animals and that the computation of the metabolism per unit of surface area fails to compensate adequately for the differences in size. Against this last theory, however, is the fact that in Rubner's two series of animals the calculations per square meter of body surface equalize the heat values for fish varying in weight from 0.5 to 245 grams and for amphibians and reptiles varying from 0.8 to 1380 grams. The only conclusion, therefore, is that activity, small though it apparently is with cold-blooded animals, is a real factor. Rubner has repeatedly commented upon the possibility of activity affecting the results obtained with cold-blooded animals. It appears as if this apprehension was fully justified. A fundamental difference existing between the two series of observations is that practically all the animals measured by Rubner or entering into his comparisons were measured either immersed in water, as in the case of fish, or in atmospheres saturated with water vapor, whereas the Nutrition Laboratory animals (except in certain experiments with the 1930 tortoises) were all measured in moderately dry atmospheres. Humidity could hardly play a great rôle at 16°. Strictly speaking, the rectal temperature should have been compared with the temperature of the environment, but in most instances only the environmental temperature was recorded. It is possible that our animals in a relatively dry atmosphere might have had a rectal temperature notably lower than the environmental temperature. The repeated instances, however, when the rectal temperature was actually measured and compared with the temperature of the environment showed but small differences in the two. The lower metabolism noted in our series as compared with that in other series upon any basis of calculation, therefore, can not be explained upon the basis of a false indication of the temperature, that is, that the temperature was not 16° but considerably lower.

#### COMPARISON OF STANDARD METABOLISM OF COLD-BLOODED ANIMALS IN NUTRITION LABORATORY SERIES WITH THAT OF COLD-BLOODED ANIMALS MEASURED BY OTHERS AT OR NEAR 30° C.

In the literature there are three instances of cold-blooded animals, in which we are especially interested, that have been actually measured at 30°, the frogs and the tortoise of Rubner<sup>1</sup> and the lizards of Martin.<sup>2</sup> The results have been computed on the basis of the heat production per kilogram of body weight and per square meter of surface area, using a surface-

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 268.

<sup>2</sup> Martin, C. J., *Philos. Trans., B*, 1903, **195**, p. 1.

area constant of 10 in all three instances. These values, together with our own observations at 30° (based upon the smoothed curves in figures 99 and 100) have been incorporated in table 118 and thus permit a direct comparison of the different groups of animals. As in table 117, the data have been arranged in the order of increasing body weights, which brings the Nutrition Laboratory series at the end. Among the tortoises in this series only the smaller tortoises having a flesh weight of approximately 3 to 4 kg. were measured at 30° C. Hence the giant tortoises do not appear in this comparison. It will be recalled that the heat production of all the animals in the Nutrition Laboratory series, when measured at 16°, was much less per unit of body weight than that of any of the other series of animals studied, a fact possibly to be explained on the

TABLE 118—*Comparison of metabolism of cold-blooded animals of different species measured at 30° C.*

Animal	Body weight	Heat produced per 24 hours		Investigator
		Per kg.	Per sq. m.	
Frog.....	46 to 50 gm.	<i>cal.</i> 15.9	<i>cal.</i> 57.0	Rubner. <sup>1</sup>
Tortoise.....	<sup>2</sup> 135 gm.	21.3	109.0	Rubner. <sup>1</sup>
Lizard.....	374 gm.	6.2	44.4	Martin. <sup>3</sup>
Lizard.....	1 kg.	5.9	59.0	Nutrition Laboratory.
Tortoise.....	<sup>3</sup> 3 to 4 kg.	5.2	73.2	Nutrition Laboratory.
Gopher snake.....	2 kg.	5.3	58.0	Nutrition Laboratory.
Rattlesnake.....	2 to 5 kg.	4.0	52.8	Nutrition Laboratory.
Boa.....	7 to 8 kg.	2.7	47.0	Nutrition Laboratory.
Python.....	15 kg.	3.0	46.0	Nutrition Laboratory.

<sup>1</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 268.

<sup>2</sup> Flesh weight.

<sup>3</sup> Martin, C. J., *Philos. Trans., B.* 1903, **195**, p. 1.

ground that only large animals were used. Here the picture is much the same. The first three animals listed in table 118, Rubner's frogs and tortoise and Martin's lizards, have the highest values per kilogram of body weight, particularly the frogs (15.9 calories) and the tortoise (21.3 calories). The values for the Nutrition Laboratory series range only from 2.7 calories with the boas to 5.9 calories with the 1-kg. lizards. The alligator was not measured at 30°, and therefore this heavy animal can not be used for comparison. In general the heat production per kilogram of body weight decreases with the increase in weight of the animal, which supports the belief that among cold-blooded animals, as with warm-blooded animals, the larger the animal the lower the heat production per unit of weight. The high value found with Rubner's frogs recalls a point raised by him, that frogs do not stand 37°, that they may have been overheated, and may have had an abnormally high metabolism.<sup>1</sup> On the other hand, he believed that the rectal temperature of the frogs might have been considerably lower than that actually indicated.

<sup>1</sup> Rubner, M., *Kraft und Stoff im Haushalte der Natur*, Leipzig, 1909, p. 91.

The values for the heat production per square meter of body surface in table 118 agree on the whole much more closely than those at 16° listed in table 117. The highest value in the entire series is 109 calories with Rubner's tortoise, and the lowest value 44.4 calories with Martin's lizards. At 30°, as at 16°, the data agree more closely on the body-surface than on the body-weight basis. It has been frequently emphasized in this discussion that the tortoise, in our judgment, has a specifically high metabolism. This, coupled with the uncertainty of computing the surface area, would make it justifiable to leave out of consideration, for the moment at least, the values for the tortoise. The other animals, varying in weight from the 46-gram frogs to the 15-kg. pythons, have heat values ranging only from 44.4 calories per square meter of body surface with Martin's lizards to 59 calories with the Nutrition Laboratory lizards. This comparison suggests a striking application of the surface-area law to the animals measured at this high temperature (30° C.), with the single exception of the tortoise. Here again the tortoise appears as a unique animal. It may be argued that any universal law should apply equally as well to tortoises as to other animals, but certainly the tortoise represents a highly specialized type of animal, with its heavy shell and its minimum surface area for vaporization of water and for the absorption or loss of heat. Undoubtedly further experimentation will throw much more light upon the heat transformation of this peculiarly constructed animal. It is more than a coincidence that the highest value at 30° found by observers other than the Nutrition Laboratory is with the tortoise of Rubner, and that the highest value in the Nutrition Laboratory series is found also with the tortoise. One can only again regret that it was impossible to have subjected the giant tortoises to this temperature.

#### COMPARISON OF STANDARD METABOLISM OF COLD-BLOODED ANIMALS IN NUTRITION LABORATORY SERIES WITH THAT OF COLD-BLOODED ANIMALS MEASURED BY OTHERS AT OR NEAR 37° C.

The tabular presentation of the metabolism measurements reported in the literature for cold-blooded animals at 16° and at 30°, under conditions of experimenting fairly comparable with those obtaining in our research, has definite value and interest, but probably those measurements made at 37° are of the greatest physiological importance, especially for comparison with the metabolism of warm-blooded animals. The cold-blooded animals, of special interest to us, whose metabolism has actually been determined by other investigators at 37° are confined to the four animals of Krehl and Soetbeer, the one tortoise of Rubner, and the lizards of Martin. The calculated values for the heat production per kilogram of body weight and per square meter of surface area for these various animals are given in table 119, arranged in the order of increasing body weights. Of the Nutrition Laboratory animals only the rattlesnakes, the boas and the pythons were heated to approximately 37°. The average body weights of these animals and the average values for the heat production per unit



of weight and of surface area are likewise given in table 119. The heat values are derived from the general curves for these three groups of snakes in figures 99 and 100. The largest heat production per kilogram of body weight is with the smallest animal, the lizard, that is, 36 calories. The smallest value, 5.9 calories, is for the pythons. The difference between these two extremes is 500 per cent of the minimum value. It is clear that the heat production per kilogram of body weight tends to decrease materially with increasing weight. The same tendency was not invariably found in the comparisons of the metabolism of cold-blooded animals per unit of weight at 16° in table 117 (p. 455), but in the comparisons at 30° in table 118 (p. 460) a decreasing heat production per kilogram of weight with increasing body weight is strikingly shown.

TABLE 119—*Comparison of metabolism of cold-blooded animals of different species measured at 37° C.*

Animal	Body weight	Heat produced per 24 hours		Investigator
		Per kg.	Per sq. m.	
		<i>cal.</i>	<i>cal.</i>	
Lizard.....	110 gm.	36.0	137	Krehl and Soetbeer. <sup>1</sup>
Tortoise.....	135 gm.	26.3	135	Rubner. <sup>2</sup>
Lizard.....	374 gm.	<sup>3</sup> 23.3 —	<sup>3</sup> 168 —	Martin. <sup>4</sup>
Frog.....	600 gm.	22.8	192	Krehl and Soetbeer. <sup>1</sup>
Alligator.....	1380 gm.	11.3	100	Krehl and Soetbeer. <sup>1</sup>
Uromastix.....	1250 gm.	9.6	82	Krehl and Soetbeer. <sup>1</sup>
Rattlesnake.....	2 to 5 kg.	7.7	91	Nutrition Laboratory.
Boa.....	7 to 8 kg.	<sup>5</sup> 6.4	<sup>5</sup> 104	Nutrition Laboratory.
Python.....	15 kg.	5.9	91	Nutrition Laboratory.

<sup>1</sup> Krehl, L., and F. Soetbeer, Arch. f. d. ges. Physiol., 1899, **77**, p. 611.

<sup>2</sup> Rubner, M., Biochem. Zeitschr., 1924, **148**, p. 281.

<sup>3</sup> Measured at 38.5° C.

<sup>4</sup> Martin, C. J., Philos. Trans., B, 1903, **195**, p. 1.

<sup>5</sup> Curves for boas in figures 99 and 100 projected by inspection from 36° to 37° C.

The values for the heat production per square meter of body surface for the tortoise of Rubner and for the frog of Krehl and Soetbeer have both been corrected, using a body-surface constant of 10 instead of 4.62. The values referred to surface area range from 192 calories with the 600-gram frog of Krehl and Soetbeer to 82 calories with the Uromastix, that is, a difference of 134 per cent. The three groups of snakes in the Nutrition Laboratory series have practically the same values, averaging 95 calories or measurably lower than the earlier observations as a whole. Nevertheless it is obvious that the uniformity between the various groups of animals is much closer on the body-surface than on the body-weight basis, and here again there is apparently definite evidence of the approximate application of Rubner's surface-area law to various cold-blooded animals. In view of the ever-present possibility of somewhat greater activity with small than with large animals and the fact that Krehl and Soetbeer made their

measurements for the most part in saturated atmospheres, it is perhaps surprising that the agreement on the whole is as close as here shown.

In elaboration of table 119 we have reported in table 120 the results of the metabolism observations at 36° or above on three individual rattlesnakes, the small Indian python, the 1931 python, and boas I and N. Although the environmental temperature reported in table 120 does not invariably represent the true rectal temperature, it can be assumed that the true cell temperature was probably not more than one or at the most two degrees below that here indicated. In the case of the 1931 python the temperature values are those for the rectal temperature and have been marked with an asterisk to distinguish them from the other records for

TABLE 120—*Metabolism of individual snakes in Nutrition Laboratory series measured at 36° C. or above*

Animal	Date	Total length of experiment	Number of periods	Days fasting	Body weight	Heat produced per 24 hours		Environmental temperature
						Per kg.	Per sq. m.	
		<i>hrs.</i>			<i>kg.</i>	<i>cal.</i>	<i>cal.</i>	<i>°C.</i>
Rattlesnake A.....	Jan. 17, 1917	1	1	?	2.95	7.32	83.1	37.3
Rattlesnake C <sup>1</sup> .....	June 29, 1917	9	1	60	5.18	<sup>11</sup> 14.63	<sup>11</sup> 199.4	36.0
Rattlesnake D <sup>1</sup> .....	July 1-2, 1917	19	5	62	3.54	<sup>11</sup> 14.65	<sup>11</sup> 178.8	38.6
Boa I.....	June 4-5, 1917	24	6	9	6.25	6.65	96.7	36.0
Boa N.....	Feb. 18, 1920	7	3	?	10.15	5.49	94.4	36.0
Small Indian python.	Feb. 27, 1917	15	5	22	5.95	8.89	129.0	37.9
Small Indian python.	Nov. 12, 1915	6	1	45	7.43	4.29	67.8	36.0
1931 python.....	Feb. 4, 1931	5	5	11	6.3	6.85	101.2	*38.7
1931 python.....	Feb. 20, 1931	4	5	27	5.7	4.59	65.8	*36.2
1931 python.....	Feb. 21, 1931	5	6	28	5.8	4.04	58.0	*36.1
1931 python.....	Feb. 24, 1931	4	5	31	5.8	4.55	65.5	*37.9

\* Rectal temperature.

<sup>1</sup> Moribund at time of observations. See page 190.

environmental temperature. Since the element of fasting plays a rôle, the number of days fasting has been indicated, according to our best estimate. The heat values per kilogram of body weight of these individual animals reported in table 120 are, except for rattlesnakes C and D, relatively uniform, irrespective of the differences in body weight, and are lower than the values given in table 119 for the animals of Krehl and Soetbeer, Martin and Rubner. The values for rattlesnakes C and D are above the values for the Uromastix and the alligator of Krehl and Soetbeer, but these two rattlesnakes were in a distinctly moribund condition at the time of the observations, as explained on page 190. The values per square meter of body surface, not including those for rattlesnakes C and D, range from 58 to 129 calories as compared with the average value of 95 calories derived from the smoothed curves for rattlesnakes, boas and pythons.

A rough approximate value for the metabolism of cold-blooded animals as a whole, when heated to a body temperature of 37°, might be considered

to be 100 calories per square meter of surface area per 24 hours. There is no evidence in tables 119 and 120 of a metabolism materially above 100 calories except in the case of the two moribund rattlesnakes, the frog of Krehl and Soetbeer, and the lizard of Martin. Whatever discussions may be raised in regard to the various values of *K* for computing the surface area, considerable latitude in this case could be permitted and yet not alter greatly the picture with regard to the comparison between the different groups of animals on the surface-area basis. Hence the data at 37°, taken as they stand in table 119, and especially when compared with the data at 30° in table 118, support the application of Rubner's law to cold-blooded animals. At 16° the heat values per unit of surface area are by no means as uniform as those at 30° and 37°, but without doubt 16° is with many species an extraordinarily low temperature and the animals at this level may rightly be considered to be more or less in stupor, with a distinctly unique metabolism. As the comparisons stand, however, certainly Rubner's surface-area law seems to be reasonably applicable at the optimum temperature for many of these cold-blooded animals, that is, 30°, and to hold with equal force at the higher temperature of 37°.

**COMPARISON OF METABOLISM MEASUREMENTS BY NUTRITION  
LABORATORY ON COLD-BLOODED ANIMALS AT TEMPER-  
ATURES FROM 15° TO 37° WITH THOSE BY KROGH  
ON OTHER COLD-BLOODED ANIMALS AT  
TEMPERATURES FROM 0° TO 28° C.**

The literature is full of observations, many of them scattered, on metabolism measurements made upon cold-blooded animals, particularly frogs, fish, and insects, at low temperatures. The extraordinary care shown by Krogh in all his zoological research leaves particular confidence in the accuracy of his measurements. Krogh's results show a degree of uniformity rarely found in other series of measurements and, since their first publication in 1914, have been often cited.<sup>1</sup> Accordingly a comparison will be made of the Nutrition Laboratory series of measurements with Krogh's series on smaller animals, because his series comprises a temperature range comparable with the lowest end of our temperature scale, that is, from 15° to 28°, and has the greater advantage of extending the observations down to 0°. For the purpose of securing the greatest degree of muscular repose, Krogh used animals that were narcotized or curarized, as well as one decerebrated toad. The strongest proof of the general accuracy and the high degree of skill exhibited in Krogh's work is the remarkable uniformity of most of his observations. This uniformity has been emphasized by Krogh in his monograph,<sup>2</sup> but we believe in a rather unfortunate manner, for although Krogh specifically states in the text the special design of his curve, it has been interpreted as indicating absolute rather than relative values. From his data we have computed the heat production per kilogram of body weight and per square meter of body surface for his various animals, using a value for *K* of 9 for goldfish and 10 for the toad and frogs. The results for the heat production per kilogram of body weight referred to temperature have been plotted in figure 101, and the same symbols have been used

<sup>1</sup> Krogh, A., *Internat. Zeitschr. f. physik.-chem. Biol.*, 1914, **1**, p. 491; Ege, R. and A. Krogh, *Internat. Revue f. Hydrobiol.*, 1914, **6**, p. 48.

<sup>2</sup> Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, p. 96.

to distinguish his animals as Krogh himself employed in his own publications. For purposes of comparison a curve has likewise been drawn in figure 101 representing the trend of the metabolism of the Nutrition Laboratory rattlesnakes. To draw any one curve to represent definitely the metabolism of all the cold-blooded animals studied by the Nutrition Laboratory might fairly be criticized. On the other hand, by inspection of figure 99 (p. 426), it can be seen that if such a curve could be drawn, it would have much the character of the curve for rattlesnakes. Therefore, the rattlesnake curve has been used tentatively, as an approximation of a general curve for all our cold-blooded animals, provided such a curve could have been legitimately drawn.<sup>1</sup> Since our tortoises had a materially different metabolic level, the straight-line curve shown in figure 97 (p. 396), representing the heat production per kilogram of flesh weight for all the tortoises, has been reproduced in figure 101 for comparison with Krogh's data.

Aside from the values for the decerebrated toad (indicated by crosses) the plotted data for Krogh's other animals lie for the most part in a reasonably regular curve. They include a narcotized frog, a curarized frog, a normal frog, a normal goldfish, and a narcotized goldfish. Reference, however, to the curve for the Nutrition Laboratory rattlesnakes and the curve for all the tortoises shows that the values for Krogh's small animals, excepting only the decerebrated toad, lie much above the metabolic level of the larger cold-blooded animals.<sup>2</sup> This bears out what has already been

<sup>1</sup> With warm-blooded animals, fasting *per se* has a specific effect after they have been a few days without food. With cold-blooded animals the interval after food ingestion when fasting begins to play a rôle is a matter not of days but possibly of weeks or, indeed, months. The small Indian python had a definitely lower metabolism in the longer fasting periods. Baldwin (Amer. Journ. Physiol., 1926, **76**, p. 196) found that when painted turtles and snapping turtles had been without food for a month they had a metabolism much lower than when freshly caught. To differentiate sharply between the metabolism obtaining during the prolonged period of digestion, the "standard metabolism" when active digestion has ceased, and the metabolism affected by prolonged fasting is not simple. In practically all our studies either the animal had been a moderately long time without food so as to have a real post-digestive metabolism, or had been a long time without food. In one instance a greatly emaciated boa showed the profound influence of long abstinence from food. The general picture is that after the digestive activity has passed there is a tendency for a lower metabolism, but not markedly lower. It is always possible that some of our curves, and it is more than probable that many of the individual periods with individual animals have been affected by varying lengths of fast, in spite of our efforts to avoid this. Hence when a curve is presented indicating the average trend of the metabolism of any group of animals, and specifically when the rattlesnake curve is used for purposes of comparison, it is to be assumed that the curve represents the metabolic trend of animals not at the peak or during the active process of digestion and not in the last stages of undernutrition.

<sup>2</sup> From the observations of Baldwin (Proc. Iowa Acad. Sci., 1927, **33**, p. 315) we have calculated that his painted turtles weighing on the average 1280 grams each (calculated flesh weight 854 grams) would have a heat production at 20° of 4.4 calories per kilogram of flesh weight per 24 hours. This is a heat production twice as high as that of our cold-blooded animals on the average at 20°, as can be seen by reference to figure 101. Since Baldwin's turtles were fairly large, one would have expected that their metabolism would more closely approximate that indicated by our rattlesnake curve. For his series of snapping turtles weighing on the average 1190 grams each (calculated flesh weight 794 grams) the heat production per kilogram of flesh weight at 20° we have calculated to be 3.3 calories, a value somewhat closer to our curve for tortoises in figure 101 than is the value for the painted turtles. The small snake of Hill (Journ. Physiol., 1911-1912, **43**, p. 379) which weighed 85 grams (the weight estimated by Rubner in his calculations) produced 0.43 gram calorie per cubic centimeter of snake per hour at 20°. Rubner (Biochem. Zeitschr., 1924, **148**, p. 295) calculated that this corresponds to 10.32 large calories per kilogram of body weight per day. This is a high metabolism compared with that of the cold-blooded animals in the Nutrition Laboratory series, but agrees reasonably well with the general trend of the metabolism of Krogh's smaller animals.

shown in tables 117 and 118, that the heat production with the larger animals is lower per kilogram of body weight than with the smaller animals. The animals of Krogh ranged in weight from 9 grams in the case of the goldfish to 35 grams in the case of the frogs, whereas the Nutrition Laboratory rattlesnakes had a minimum body weight of 3 kg., and the rattlesnake curve represents the general trend of metabolism for animals having an average weight even greater. It is thus clear that the heat production per kilogram of body weight, especially in the temperature range

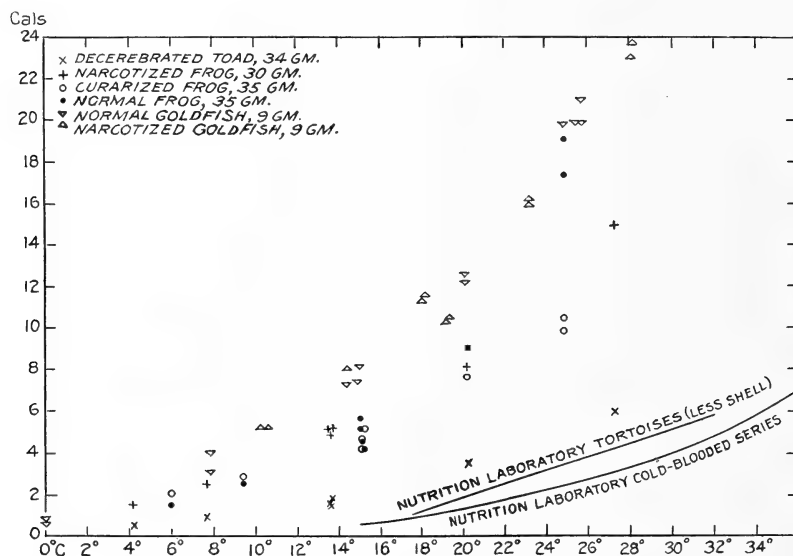


FIG. 101—COMPARISON OF STANDARD HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS (REFERRED TO ENVIRONMENTAL TEMPERATURE) OF COLD-BLOODED ANIMALS IN KROGH SERIES AND THOSE IN NUTRITION LABORATORY SERIES.

Curve for Nutrition Laboratory tortoises represents both 5-kg. and giant tortoises, on basis of flesh weight. Curve entitled "Nutrition Laboratory cold-blooded series" is curve for rattlesnakes, which is considered to represent, on the average, general trend of metabolism of all cold-blooded animals in Nutrition Laboratory series except tortoises. Plotted circles, triangles, crosses, etc., are for Krogh's animals, the identity of which is explained in upper left-hand corner of chart.

over which both Krogh's small animals and ours were measured, that is, from 15° to 28°, is much higher with the small than with the larger animals.

The calculations of the heat production per square meter of surface area, employing the constants mentioned on page 464, have been made for Krogh's animals and plotted in figure 102, with reference to the environmental temperature. The Nutrition Laboratory curve for rattlesnakes has likewise been included, as representative of all our cold-blooded animals, and again a straight-line curve representing the so-called "5-kg." tortoises. The giant tortoises are not included in this curve, because they were measured at only one temperature. There is a striking difference between

the comparison per kilogram of body weight and that per square meter of surface area, for on the latter basis practically all Krogh's values between  $15^{\circ}$  and  $28^{\circ}$  lie reasonably close to our average lines for large cold-blooded animals. Only the decerebrated toad presents (as in all comparisons in which it appears) an unusual metabolism.<sup>1</sup> Indeed, the curve for Krogh's

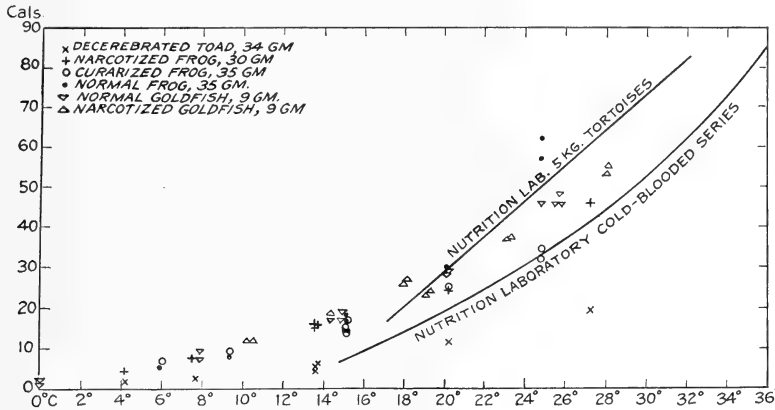


FIG. 102—COMPARISON OF STANDARD HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS (REFERRED TO ENVIRONMENTAL TEMPERATURE) OF COLD-BLOODED ANIMALS IN KROGH SERIES AND THOSE IN NUTRITION LABORATORY SERIES.

Curve for Nutrition Laboratory tortoises represents only 5-kg. tortoises, on basis of body surface calculated from flesh weight. Curve entitled "Nutrition Laboratory cold-blooded series" is curve for rattlesnakes, which is considered to represent, on the average, general trend of metabolism of all cold-blooded animals in Nutrition Laboratory series except tortoises. Plotted circles, triangles, crosses, etc., are for Krogh's animals, identity of which is explained in upper left-hand corner of chart. At  $15^{\circ}$  and  $20^{\circ}$  there are several plotted points for the normal frog that are not shown clearly because of amount of reduction of chart.

animals could almost be superimposed on our series, lying, to be sure, slightly above the rattlesnake curve but certainly between that and the curve for tortoises. The significance of this comparison is twofold. In the first place, it shows clearly that the heat production per square meter of surface area is strikingly uniform even with animals varying so greatly in size as from 9 grams (Krogh's goldfish) to 3, 5 and 32 kg. (Nutrition Laboratory animals). Thus further evidence is furnished with regard

<sup>1</sup>The extraordinarily low metabolism of this decerebrated animal raises the question as to the rôle played by the brain in the energy metabolism. Of vital interest in this connection are the observations made by Talbot (*Arch. Pediatrics*, 1915, **32**, p. 452) on an infant with congenital absence of the cerebral hemispheres. Talbot found with this child, of essentially normal weight and height, a very low metabolism. Indeed, the heat production, both per kilogram of body weight and per square meter of body surface, was only about 60 per cent of that noted with a normal child of approximately the same age, weight and height. To what extent this low metabolism is due to the degree of repose of the infant and to what extent to a real depression of the metabolism owing to the absence of the cerebral hemispheres is still to be settled. Krogh has commented upon the fact that his animals all remained quiet during the period of experimentation, and yet his decerebrated toad has a metabolism much lower than that of any of the others. These two facts, we believe, are highly suggestive and undoubtedly are of significance in the interpretation of the rôle the brain may play in the metabolic processes.

to the applicability of Rubner's surface-area law to cold-blooded animals.<sup>1</sup> The special value, however, of this comparison lies in the fact that subsequently use can legitimately be made of the probable trend of the metabolism of cold-blooded animals below the temperature at which we had to cease our observations. If the results for our large animals and Krogh's small animals agree so closely between 15° and 28°, as they do in figure 102, it is reasonable to suppose that values below 15° in the Krogh series would be, theoretically at least, equally comparable with values that might have been obtained on our larger animals at these lower temperatures. On the whole, therefore, Krogh's observations in a striking way supplement our measurements on the larger animals. To be sure, in Krogh's series his decerebrated toad represents an exceptional instance and in our series the giant tortoises give aberrant results, but on the whole the picture is reasonably uniform. In the literature there are a number of instances (reference to which will be made later) when measurements were made at or about 10° upon animals that we wish to compare with this series. It would appear justifiable to compare these measurements with a curve drawn through the Krogh material, which at 10° would lie not far from 8 or 9 calories per square meter of body surface. It is highly probable that this value would be not far from that which could have been expected from our larger animals, provided we had dared to risk cooling them to this low temperature.

It is obvious from figure 102 that the Krogh series at the lower temperatures is not a direct projection of the curve for our rattlesnakes, and it is only with considerable reserve that one can state that a surface-area law mathematically applies to these very small animals. Certainly, however, when the comparisons are made between the metabolism per unit of weight and of surface area, it can be seen that the relationships are much closer between the large and the small animals on the surface-area basis. In general, the Krogh curve would lie somewhat above the hypothetical curve for all our animals, represented by the curve for rattlesnakes. In view of the depressing effect of fasting with warm-blooded animals and the indication, at least with our small Indian python, that prolonged fasting has an effect upon the metabolism of these cold-blooded animals, one would have expected that, because of the fairly long period that Krogh's animals had been without food (all of them for at least a month and some for the whole winter), his values would have been low rather than high. It is probable, however, that the calculation of the heat

<sup>1</sup> Bodine (*Journ. Expt. Zool.*, 1921, **32**, p. 157) found that the carbon-dioxide production was directly proportional to the two-thirds power of the body weight with extraordinary regularity in grasshoppers weighing from 0.94 to 2.16 grams, and he concludes that the surface-area law holds for grasshoppers as well as for mammals. We have calculated that the painted turtles of Baldwin (*Proc. Iowa Acad. Sci.*, 1927, **33**, p. 315) produced on the average 42 calories per square meter of body surface (calculated from the flesh weight) per 24 hours at 20° and his snapping turtles 30.5 calories. This latter value coincides exactly with the metabolism at 20° indicated by our curve for the 5-kg. tortoises. Hill's snake (*Journ. Physiol.*, 1911-1912, **43**, p. 379) we have computed to have at 20° a heat production per unit of surface area of 36.3 calories, which is in reasonably good agreement with the metabolism at 20° indicated by our curves for cold-blooded animals in figure 102. All these comparisons show a much closer uniformity in the metabolism referred to body surface than in that referred to body weight.

production per square meter of surface area, using the two-thirds power of the body weight as the exponent in the body-surface formula, may not completely equalize the differences in size of the animals, and it is probable that had his animals not been without food so long, his curve would be even a little higher. But even if allowances are made for differences due to nutritive state, it is obvious that Krogh's data agree with our data much more closely on the surface-area than on the body-weight basis. Some of the difference between the levels of Krogh's data and the rattlesnake curve (which represents all the Nutrition Laboratory animals) may be attributable to the use of the body-surface constant.<sup>1</sup> For all our snakes we used a factor of 12.5 and for the alligator 12.6. Only with our lizards and tortoises (flesh weight) was the lower constant of 10 used. For Krogh's animals we employed constants of 9 and 10. Obviously if a K of 10 had been used for our snakes, this would have raised the level of the general curve for our animals throughout its entire length about 20 per cent and would have brought it somewhat more into conformity with the Krogh curve (see page 471).

The heat values for our cold-blooded animals per unit of weight and per unit of surface area are lower in general than those of the other investigators that we have cited. It is easy to find a metabolism value above the minimum, because of the influence of activity. Our results are probably the least contaminated by the extraneous factors of digestion, muscular activity, and agitation. The conclusions drawn by other investigators regarding cold-blooded animals have thus far, for the most part, been based upon measurements with animals other than snakes. We purposely chose the snake because it is perhaps the quietest of the cold-blooded animals and presents the least complication so far as activity is concerned. With regard to the influence of digestion, every precaution was taken to secure information, so far as possible, regarding the exact time when our animals last fed prior to the metabolism measurements, although, as Rubner<sup>2</sup> has emphasized, one of the great difficulties of working with cold-blooded animals is that the nutritive condition can not be controlled. Rubner had to use for his comparisons animals that had been fasting different lengths of time. Indeed, with most of his cold-blooded animals other than the fish, probably the length of fasting was unknown. Buytendijk<sup>3</sup> states that his snakes and lizards had had no food on the day preceding the metabolism experiment, that his ring snakes had eaten nothing for some months, and the two boas had had no food for a fortnight. If the influence of the

<sup>1</sup> A most illuminating consideration of the general uniformity of the constants used in computing surface area is shown in the tabular presentation by E. Krauss (*Lehrbuch der Stoffwechselmethodik, I, Methodik d. Energie- u. Stoffwechsels*, Leipzig, 1928, table 20, p. 369). His table shows that in practically all cases the constant lies close to 10. The exceptions are Giaja's constant of 6.54 for the hen, Inaba's constant of 18.6 for the adder, and Rubner's constant of 4.6 for the frog. See, also, Klein, W., and M. Steuber, *Die gasanalytische Methodik des dynamischen Stoffwechsels*, Leipzig, 1925, table 11, p. 98. As we go to press there has appeared, unfortunately too late for us to analyze critically, a report of the extensive studies of Terroine and Delpech (*Annal. de Physiol.*, 1931, **7**, p. 341) on frogs, fish, eels, and turtles.

<sup>2</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 223.

<sup>3</sup> Buytendijk, F. J. J., *Proc. Section of Sci., Royal Acad. Sci., Amsterdam*, 1910, **13**, (1), p. 48; *ibid.*, *Kon. Akad. v. Wetensch., Wis-en Natuurk. Afd.*, 1910, **18**, p. 870.



state of nutrition is as pronounced as Rubner believes, Buytendijk's data represent another illustration of the difficulty of comparing different animals at different stages of fasting or nutrition. It is believed that the nutritive state of our animals was as well, if not better, known with relation to the previous ingestion of food than that of any of the other cold-blooded animals thus far studied. But although our findings are consistently lower than those of others, they can be looked upon as representing more nearly the true physiological, internal processes of the cold-blooded animal, uncomplicated by muscular activity, agitation, or digestion.

### SURFACE-AREA LAW

Perhaps no one finding in this entire study has been any more astounding than the definitely shown fact that, with the single exception of the giant tortoises (an exception that must not be forgotten), the heat production of all our cold-blooded animals is extraordinarily uniform when computed on the basis of the calculated surface area, employing the two-thirds power of the weight times a constant. Attention is further challenged by the fact that not only do our large animals have this uniformity among themselves but the extraordinary series of observations by Krogh with small animals averaging about 30 grams in weight (omitting the decerebrated toad) shows an agreement in the values per square meter of computed surface area that is strikingly in accord with the values for our large animals. The variability in the *average* heat production per square meter of body surface of the different groups of cold-blooded animals at any given temperature is rarely 100 per cent (fig. 102, p. 467). On the other hand, with warm-blooded animals measured at or about the critical temperature, the heat production per square meter of surface area per 24 hours may range from approximately 600 calories with a small rat or a dove to as high as 1700 calories or more with the larger domestic animals, such as the steer, the cow and the horse. In other words, with cold-blooded animals varying in weight three-thousand fold, *i.e.*, from 9 grams to 32 kilograms, the uniformity in metabolism per square meter of surface area at a given temperature is two or three times closer than it is with warm-blooded animals of similar disparity in weight. Thus it would appear as if the surface-area law were established more definitely with the entire series of cold-blooded animals than with the warm-blooded animals.

The only conceivable argument, however, that the surface-area relationship represents a thermal law with cold-blooded animals would be that, since their body temperature is usually a little below the environmental temperature, they tend to absorb heat from the environment in proportion to their surface area. Most of Krogh's experiments were carried out with fish and other animals immersed in water, a medium for the rapid transfer of heat. Most of our measurements were made in relatively dry air. Other measurements, such as those by Krehl and Soetbeer, have been made in saturated atmospheres, and relatively few have been made with low humidity. Since the absorption of heat from the environment prevails primarily only at high temperatures and low humidity, it is difficult to think of a surface-area law applying with cold-blooded animals in the sense

of a thermal law, save under extremely special conditions where heat may be absorbed from the environment. As has been pointed out, the vaporization of water is without doubt the greatest, if not the sole, method for heat loss with cold-blooded animals, but this is undoubtedly distributed in an as yet unknown proportion between the lungs and the skin, and although probably skin area does play a rôle in affecting that proportion lost from the skin, the area of the lungs (a factor as yet almost entirely disregarded in considering the surface-area relationships with warm-blooded animals) must also play a rôle. This leads to the conviction that in all probability the surface area as such is only one of a great many factors in the morphological law of growth or development, which is perhaps best expressed by approximately the two-thirds power of the body weight.<sup>1</sup> The surface-area relationships noted with warm-blooded animals likewise in all probability have to deal more with the morphological structure of the various animals. The morphological structure, together with other factors affecting metabolism, will be discussed subsequently (pages 508 to 517).

Examination of the body-surface constants used for various animals, both cold-blooded and warm-blooded, shows that for the most part they are close to 10, the lowest values being those of Buytendijk of 7 and 8 for the shark and the highest those for snakes of about 12.5 to 13.<sup>2</sup> Certainly the variability in the constant is much less than the differences in the heat production per square meter of surface area noted with the various groups of warm-blooded animals. Since the two-thirds power of the body weight may represent a morphological law of growth and since the surface area represents practically the two-thirds power of the body weight times a constant,  $K$ , which is usually not far from 10, it is still legitimate for purposes of comparison (and certainly very convenient for comparison with earlier data in the literature) to express the metabolism values found with any of the animals, cold-blooded or warm-blooded, on the basis of the heat production referred to the two-thirds power of the weight multiplied by 10. In this way numerical units are obtained that are relatively comparable with the earlier expressions of the heat production per unit of surface area.

All the heat values per square meter of body surface of Krogh's animals, except the goldfish, we computed on the basis of a surface-area constant of 10. We have therefore recomputed the values for the goldfish on the basis of a  $K$  of 10 and have likewise replotted our rattlesnake curve (which represents the general trend of the metabolism of all the cold-blooded animals in the Nutrition Laboratory series) on this same basis, that is, elevating the location of the curve 20 per cent. This corrected curve has then been blended with a curve drawn to represent the Krogh material, and the resulting composite curve is reproduced in figure 103. This composite curve may be considered to indicate with considerable accuracy the

<sup>1</sup> An exception to the general belief that the two-thirds power of the body weight represents a general morphological law of growth is found in the observations of Fry (Quart. Journ. Expt. Physiol., 1913, 7, p. 185), who notes that the blood volume in lizards and frogs of varying size conforms much more closely with  $w^{1.21}$  and concludes that the blood volume is neither proportional to the body surface, as in warm-blooded animals, nor to the body weight, but does appear to be proportional to the weight of the osteo-muscular system.

<sup>2</sup> Extremes in use of body-surface constants have already been mentioned in footnote on page 469.

standard heat production (large calories) per 24 hours of all cold-blooded animals of whatever size, at different body (cell) temperatures, referred to the two-thirds power of the body weight (in grams) times 10, and divided by 10,000 to approximate the calculated surface-area in square meters. It will be noted that at 37° the heat production on this basis is 110 calories. For convenience the absolute values on this basis for each 2-degree temperature interval from 4° to 37° have been derived from the curve and summarized in table 121.

If the surface-area relationship does not represent a thermal law, it may be proper at this time to question whether some other designation than

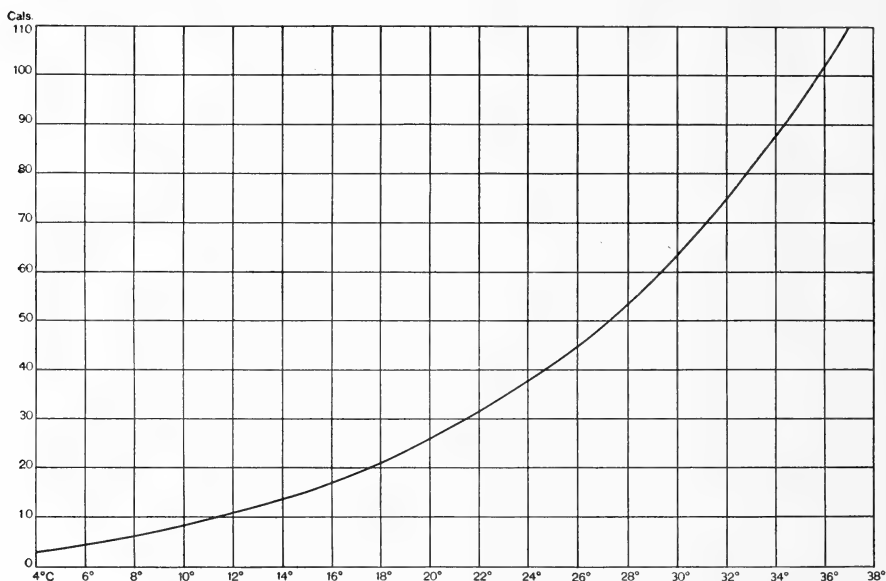


FIG. 103—STANDARD HEAT PRODUCTION PER 24 HOURS OF COLD-BLOODED ANIMALS IN GENERAL, REFERRED TO BODY OR CELL TEMPERATURES BETWEEN 4° AND 37° C.

Heat production as represented by this curve has been calculated per 24 hours and per unit of body weight (in grams) raised to two-thirds power, multiplied by 10, and divided by 10,000 (approximately the calculated surface area in square meters).

“heat per square meter of surface area” is not justifiable when referring to these values. For practical purposes undoubtedly this phraseology will be used for some time, but it is well worth while considering whether some other expression devoid of any implied specific relationship between surface area and heat exchange should not be employed. The surface-area conception has been of invaluable service. It brought order out of chaos and showed that with warm-blooded animals a relationship exists between the *calculated* surface area and the heat loss. With cold-blooded animals, on the contrary, although there is apparently a relationship between the *calculated* surface area and the heat production, there is certainly no proof that the surface area controls the heat loss. To be sure, the cold-blooded animal loses heat by vaporization of water, partly from the lungs and

partly from the skin, the loss varying with the temperature and the humidity of the environment and possibly likewise with the wind velocity. But all the evidence available indicates that, save under exceptional conditions, such as during digestion, incubation, and agitation, there is no loss of sensible heat from the body surface since practically the entire heat loss takes place through the vaporization of water. The surface-area conception therefore ceases to have its original importance, and a search for a more scientific basis for comparisons of the metabolism of animals of different sizes and different species must be actively carried on. The comparisons must be shifted from a consideration of heat loss

TABLE 121—*Heat produced per 24 hours at different body temperatures by cold-blooded animals in general, for each unit of body weight (in grams) raised to two-thirds power, multiplied by 10, and divided by 10,000 to approximate calculated surface area in square meters*

Tempera- ture	Calories per $w^{2/3} \times 10$	Tempera- ture	Calories per $w^{2/3} \times 10$
°C.		°C.	
4	3.0	22	32.0
6	4.5	24	38.0
8	6.5	26	45.0
10	8.5	28	54.0
12	11.0	30	63.5
14	13.5	32	75.0
16	17.0	34	88.0
18	21.0	36	102.0
20	26.0	37	110.0

(surface-area law) to a consideration of heat production, and it will be desirable to refer the metabolism to some thermogenetic unit, in contradistinction to the surface-area unit, which implies heat loss. It is our intention to analyze in another place the findings of the Nutrition Laboratory on both warm-blooded and cold-blooded animals from this standpoint. In this report we content ourselves with raising the question, and complete our discussion by retaining the surface-area figures in the interest of uniformity of treatment. It is believed, however, that the apparent relationship between heat production and surface area is wholly fortuitous.

## COMPARISON OF METABOLISM OF COLD-BLOODED ANIMALS WITH THAT OF WARM-BLOODED ANIMALS, CELL TEMPERATURE OF WHICH HAS BEEN LOWERED BELOW 37° TO APPROXIMATE THAT OF COLD-BLOODED ANIMALS

Since, as stated in the introduction of this report, our chief interest in studying cold-blooded animals was to secure information that would help to illuminate the energy problems in human physiology, it follows that one of the chief features of the analysis of our results obtained with cold-blooded animals is the application of the findings to the interpretation of the laws governing heat production and heat loss in living organisms, specifically warm-blooded animals and especially man. All animals have, in common, chemical and energy transformations accompanied by oxygen consumption, carbon-dioxide production, and heat production. It becomes of importance, therefore, to compare the heat production of cold-blooded animals with that of warm-blooded animals.

The reaction of cold-blooded animals to changes in environmental temperature is of such a type that as the environmental temperature falls, the cell temperature and the metabolism of the cold-blooded animal decrease. Under normal conditions the reaction of the warm-blooded animal to decreasing environmental temperatures is of a markedly different nature. In the first place, with many warm-blooded animals lowering of the environmental temperature results in the bringing into play what has been termed by Rubner as the "chemical heat regulation," which calls immediately for an increase in the metabolism. This chemical heat regulation obtains so long as the cell temperature is not materially altered. With greatly decreased environmental temperature there comes a time when the chemical regulation breaks down, the animal can no longer combat the loss of heat due to the cold, and succumbs to it, with a rapidly falling rectal temperature. Under these conditions, even with the warm-blooded animal, when the rectal temperature falls there is a lowering of the metabolism corresponding, though with markedly different quantitative relations, to the lowering of the metabolism of the cold-blooded animal. Conversely, when there is an increase in environmental temperature, the physical heat regulation of the warm-blooded animal is called into play, and the animal maintains its body temperature usually constant at about 37°. If there is a marked rise in environmental temperature and any factor is introduced that interferes with physical regulation, there is finally an increase in the cell temperature, and this in turn results in an increase in the metabolism, precisely as the increase in the cell temperature of the cold-blooded animals results in an increased metabolism. In the last analysis, therefore, the two groups of animals act qualitatively in the same way. The warm-blooded animals, however, are provided with a chemical heat regulation that prevents a rapid fall in body temperature in cold environments, and likewise with a physical heat regulation, consisting in large part of vaporization of water, which prevents a rapid increase in cell temperature in warm or hot environments. With the cold-blooded animal likewise, the vapor-

ization of water tends to lower its cell temperature so that, when studied under conditions where physical regulation can obtain, it does not attain completely the temperature of the environment. Because of these points of similarity in the reaction of warm-blooded and cold-blooded animals to environmental temperature, physiologists for many years have attempted to compare the effects of different temperatures upon the heat production of these two great divisions of animals.

In comparing the metabolism of cold-blooded and warm-blooded animals at the same cell temperature, two different methods have been employed. The one depends upon lowering the body temperature of the warm-blooded animal a number of degrees, to bring it into the range of the normally occurring body temperature of the cold-blooded animal. The second method is to raise the cell temperature of the cold-blooded animal until it is not far from 37°, the cell temperature of most warm-blooded animals and specifically man. As regards the first of these methods, the body temperature of the warm-blooded animal can be lowered artificially in a number of ways, by cutting or pithing the spinal cord, by placing the animal under the influence of some drug, especially curare, or by subjecting the animal to extreme cold, such as an ice bath. A few of the warm-blooded animals undergo hibernation, a normal condition occurring with the change in seasons, when the cell temperature also is lowered. The experiments on the influence of curare are perhaps best exemplified by the most careful study of Krogh with the dog.<sup>1</sup> The effect upon the metabolism of severing the spinal cord has been studied more especially by Grafe and Freund,<sup>2</sup> and the method of subjecting the warm-blooded animal to severe cold has been employed by Pflüger<sup>3</sup> and more recently by Giaja.<sup>4</sup> Extensive studies have been made of the hibernating animal and a great deal has been written about them, but unfortunately few experiments have been made in which the metabolism of an animal during actual winter sleep has been measured. Rubner<sup>5</sup> has presented in detail his calculations of the results of Nagai<sup>6</sup> on the metabolism of hibernating marmots. Mareš<sup>7</sup> has reported in even more detail, although in a less accessible publication, his observations on the hibernating marmot. Pembrey<sup>8</sup> and his associates likewise have published data regarding the gaseous metabolism during winter sleep.

Severe criticisms may be raised against the artificial lowering of the cell temperature of warm-blooded animals. Thus, the effect of curare is to rule out all muscular activity and under curare the animal may be considered to be in an unphysiological condition requiring artificial respiration. To be sure, Krogh<sup>9</sup> has shown that the metabolism of fish is the same whether

<sup>1</sup> Krogh, A., *Internat. Zeitschr. f. physik.-chem. Biol.*, 1914, **1**, p. 491; *ibid.*, *The Respiratory Exchange of Animals and Man*, London, 1916, p. 94.

<sup>2</sup> Freund, H., and E. Grafe, *Arch. f. d. ges. Physiol.*, 1917, **168**, p. 1.

<sup>3</sup> Pflüger, E., *Arch. f. d. ges. Physiol.*, 1878, **18**, p. 247.

<sup>4</sup> Giaja, J., *Ann. de Physiol.*, 1925, **1**, p. 596.

<sup>5</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, pp. 303 *et seq.*

<sup>6</sup> Nagai, H., *Zeitschr. f. allg. Physiol.*, 1909, **9**, p. 243.

<sup>7</sup> Mareš, F., *Bohemian Arch. Med.*, *Journ. Advancement Med. Sci.*, Prague, 1889, **2**, pp. 458-527; *ibid.*, *Compt. Rend. Soc. de Biol.*, 1892, 9th ser., **4**, p. 313.

<sup>8</sup> Pembrey, M. S., and W. H. White, *Journ. Physiol.*, 1895, **18**, p. xxxv; *ibid.*, *Journ. Physiol.*, 1895-1896, **19**, p. 477; Pembrey, M. S., *Journ. Physiol.*, 1901, **27**, p. 66; *ibid.*, *Journ. Physiol.*, 1903, **29**, p. 195.

<sup>9</sup> Ege, R., and A. Krogh, *Internat. Revue f. Hydrobiol.*, 1914, **6**, p. 48.

narcotized or not, but the necessity for artificial respiration in the case of the curarized animal, the uncertainty of the ventilation of the lungs, the lability of the carbon-dioxide storage, and particularly the abnormally low respiratory quotients prevailing at low temperatures, make the calculation of the heat production from the measured gaseous exchange under such conditions extremely uncertain. Pithing calls for an operative procedure and special temperature control, and hence also results in an abnormal condition. With the hibernating animal the situation is entirely different. Hibernation is for a number of animals a normal physiological process. The only drawback to observations during hibernation is that, practically, the determination of the metabolism is most difficult. The tendency has been to use an apparatus much too large for the small amounts of carbon dioxide and oxygen actually participating in the metabolism of the animal while in winter sleep. This procedure is, we believe, distinctly open to criticism and for this reason we have ruled out any consideration of the studies of Pembrey and of Weinland and Riehl.<sup>1</sup> Usually a low respiratory quotient in the transition stage between sleep and awakening is reported. There is a marked alteration in metabolism, with an accompanying disturbance of the regularity in the carbon dioxide exhaled. Frequently the same apparatus has been employed to study the metabolism both when the animal was awake and when asleep, and since the metabolism of the animal awake may be one hundred times greater than that during sleep, the same technique is usually not at all suitable for both measurements. Entirely aside from the technical difficulties of measuring the metabolism, however, the special conditions (except for hibernation) to which warm-blooded animals have been subjected in order to lower their body temperature introduce such an abnormal element in their usual physiological processes that the value of the results may be legitimately questioned. This point has been emphasized by Rubner,<sup>2</sup> who maintains that hibernation is the only wholly normal condition under which the effect of environmental temperature upon the metabolism of warm-blooded animals can be studied. These criticisms must not be forgotten in making any comparison between cold-blooded and warm-blooded animals at low body temperatures.

Of the methods for artificially lowering the cell temperature of the warm-blooded animal, too little evidence is available regarding the effects of extreme cold, such as ice baths, and our comparison of warm-blooded and cold-blooded animals at low cell temperatures will therefore be confined, so far as the warm-blooded animals are concerned, to observations obtained by means of curare, pithing, and hibernation. In the literature there are frequent references to observations dealing with these problems by various investigators, but it will be sufficient for our purpose to consider only a few typical examples. For the curarized animal we have chosen the extremely careful measurements of Krogh<sup>3</sup> on the dog and Velten's<sup>4</sup> measurements

<sup>1</sup> Weinland, E., and M. Riehl (*Zeitschr. f. Biol.*, 1907, **49**, p. 37) have pointed out clearly the difficulties of determining the metabolism from a small gain or loss in weight of a large container.

<sup>2</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, p. 303.

<sup>3</sup> Krogh, A., *loc. cit.*

<sup>4</sup> Velten, W., *Arch. f. d. ges. Physiol.*, 1880, **21**, p. 361.

on the rabbit, for the pithed animal the determinations by Krarup<sup>1</sup> with the rabbit, and for the hibernating animal the measurements of Nagai<sup>2</sup> on the marmot (cited in detail by Rubner<sup>3</sup>), and the painstaking series of measurements on marmots by Mareš.<sup>4</sup> For the cold-blooded animals, the comparison will include the series of observations by Krogh<sup>5</sup> on small animals and the series by the Nutrition Laboratory on larger animals.

A factor for the most part ignored in comparisons of this kind is the influence of size. The comparison of a hibernating marmot weighing 3 kilograms with that of cold-blooded animals weighing from 50 to 1000 grams presents a real problem. Can the comparison be made by computing the metabolism per kilogram of body weight? Should it be made by referring the metabolism to the calculated surface area or simply to the two-thirds power of the body weight? These three methods of expression appear constantly throughout the literature. It is conceivable that differences in size might be avoided by comparing the metabolism of a warm-blooded animal in winter sleep with that of a cold-blooded animal of the *same body weight*. But even under such conditions there may be differences (of great significance to some writers) in the actual surface areas of the animals, depending upon the "body-surface constant." In general, the formula  $S=K \times w^{2/3}$  obtains, and the only variant of any moment is the factor K. With practically all animals, both warm-blooded and cold-blooded, however, a K of 10 would be sufficiently close for purposes of comparison, at least to note if there is any great difference between the metabolism of the cold-blooded and that of the warm-blooded animal. Rubner maintains that the surface-area conception, although obtaining, for example, with different forms of fish, does not obtain with cold-blooded animals of different species. But the comparison of the smoothed curves representing the general trend of the metabolism of the cold-blooded animals studied by the Nutrition Laboratory, not only among themselves but particularly with reference to the observations of Krogh on smaller cold-blooded animals, shows that the comparison of the metabolism of animals of different sizes with reference to body surface is justifiable, not only among animals of the same species but among animals of different species. Our comparisons, therefore, of the metabolism of warm-blooded and cold-blooded animals at low body temperatures will be made both upon the basis of the heat production per kilogram of body weight and upon the basis of the heat production per square meter of body surface. The first method of comparison is certainly open to no objection if the animals are of essentially the same body weight, and the second method has been advocated by Rubner when there are great differences in weight.

<sup>1</sup>Krarup, J. C., *The Influence of Temperature on the Respiratory Metabolism or Heat Production*, Dissert., Copenhagen, 1902 (In Danish). See, also, Krogh, A., *The Respiratory Exchange of Animals and Man*, London, 1916, p. 94.

<sup>2</sup>Nagai, H., *loc cit.*

<sup>3</sup>Rubner, M., *loc cit.*

<sup>4</sup>Mareš, F., *loc cit.*

<sup>5</sup>Krogh, A., *Internat. Zeitschr. f. physik.-chem. Biol.*, 1914, **1**, p. 491; Ege, R., and A. Krogh, *Internat. Revue f. Hydrobiol.*, 1914, **6**, p. 48.



# COMPARISON OF METABOLISM OF COLD-BLOODED ANIMALS WITH THAT OF WARM-BLOODED ANIMALS WHOSE CELL TEMPERATURE HAS BEEN LOWERED BY CURARE OR BY SEVERING OF SPINAL CORD

In figure 104 have been plotted the metabolism data for Krogh's curarized dog, Velten's curarized rabbit, and Krarup's pithed rabbit, calculated per

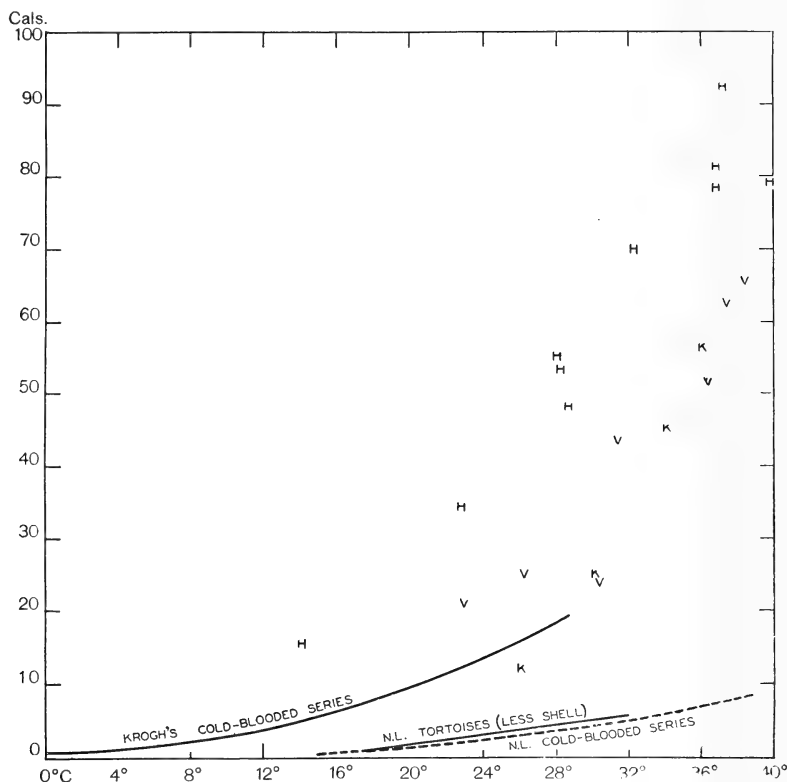


FIG. 104—HEAT PRODUCTION PER KILOGRAM OF BODY WEIGHT PER 24 HOURS (REFERRED TO ENVIRONMENTAL OR RECTAL TEMPERATURE) OF COLD-BLOODED ANIMALS COMPARED WITH THAT OF CURARIZED OR PITHED WARM-BLOODED ANIMALS.

Curve for Nutrition Laboratory tortoises represents both 5-kg. and giant tortoises, on basis of flesh weight. Curve entitled "N. L. cold-blooded series" is curve for rattlesnakes, which is considered to represent, on the average, general trend of metabolism of all cold-blooded animals in Nutrition Laboratory series, except tortoises. Curve for Krogh's cold-blooded series is for small animals of from 9 to 35 grams. Data for Krogh's curarized dog are indicated by letter H, those for Velten's curarized rabbit by letter V, and those for Krarup's pithed rabbit by letter K.

kilogram of body weight per 24 hours and referred to the *body* temperature. The results for the dog have been indicated by the letter H, employing the same designation used by Krogh in his presentation of his data for this animal. The values for Velten's rabbit are represented by the letter V and those for Krarup's rabbit by the letter K. In all instances the heat pro-

duction was computed from the measured oxygen consumption. The data for Krarup's rabbit represent the 2925-gram rabbit studied at body temperatures as low as  $26^{\circ}$ , in his experiment No. XIX. In addition to these data, figure 104 includes a curve representing the trend of the metabolism per kilogram of body weight of the small cold-blooded animals studied by Krogh. This curve has been based upon the data plotted in figure 101 and extends over temperatures ranging from  $0^{\circ}$  to  $28^{\circ}$ . The curve indicating the trend of the metabolism per unit of weight of the Nutrition Laboratory rattlesnakes between  $15^{\circ}$  and  $40^{\circ}$  has likewise been chosen for comparison, as representing *in general the average trend of the metabolism of all the cold-blooded animals in this series*. Finally a straight-line curve indicating the trend of the metabolism per unit of flesh weight of all the tortoises, both the 5-kg. and the giant animals in the Nutrition Laboratory series, and extending from  $17^{\circ}$  to  $32^{\circ}$ , has been included.

The striking difference in the heat production per kilogram of body weight between the small cold-blooded animals of Krogh and the larger cold-blooded animals in the Nutrition Laboratory series has already been shown clearly in figure 101. The difference between the metabolism of the cold-blooded animals and that of the curarized and pithed warm-blooded animals per unit of weight was found to be so great that, in plotting the comparisons in figure 104, the scale for the ordinates had to be made to represent an increase in heat production for each square five times as great as that in figure 101. The difference between the metabolism per kilogram of body weight of the cold-blooded series of Krogh and that of the Nutrition Laboratory is explained by the great difference in the body weights of the two groups of animals. The average weight of Krogh's small cold-blooded animals was about 30 grams. Krogh's dog weighed approximately 950 grams and Velten's rabbits from 1.5 to 2.5 kg. Krarup's rabbit weighed 2.9 kg., which is not far from the average weight of Velten's rabbits. In other words, the warm-blooded animals all weighed much more than Krogh's cold-blooded animals. Since in figure 104 the relationship between metabolism and body weight (not surface area) is considered, the difference between the results for the warm-blooded animals and the results for Krogh's cold-blooded animals is greater than would be expected, for of two groups of animals at the same rectal temperature one would suppose that the higher metabolism per unit of weight would be found with the smaller animals. The warm-blooded animals, however, have in practically every case a metabolism per kilogram of body weight much greater than that of the small cold-blooded animals studied by Krogh and enormously greater than the metabolism on the body-weight basis of the large cold-blooded animals in the Nutrition Laboratory series. The only instance where the metabolism per kilogram of body weight of the warm-blooded animal under these special conditions is at all comparable with that of the cold-blooded animals is with the rabbit of Krarup at  $26^{\circ}$ , the heat production of which has been calculated to have been 11.8 calories. According to the curve for Krogh's small (30-gram) cold-blooded animals, the heat production at  $26^{\circ}$  would be about 16 calories. In this instance the difference in body weight, which was large (Krarup's rabbit being nearly

one-hundred times heavier than Krogh's cold-blooded animals), accounts in part for this seeming agreement. But in general the picture shown in figure 104 is that the warm-blooded animal, subjected to a lowered rectal temperature by means of curare or pithing, has a metabolism per unit of weight much greater than that of cold-blooded animals of the same cell temperature, notwithstanding the extreme differences in body weight and

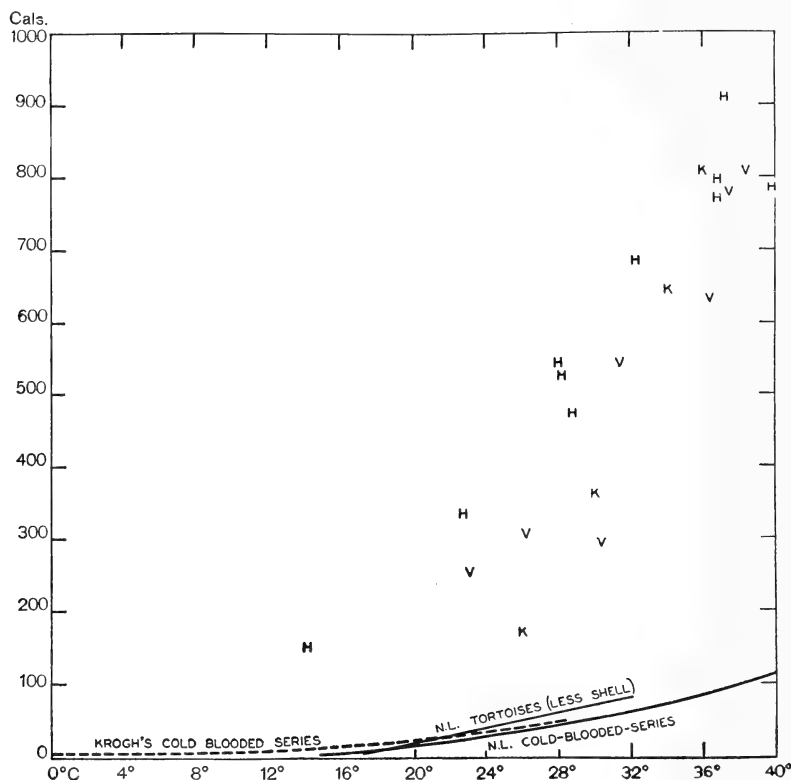


FIG. 105—HEAT PRODUCTION PER SQUARE METER OF BODY SURFACE PER 24 HOURS (REFERRED TO ENVIRONMENTAL OR RECTAL TEMPERATURE) OF COLD-BLOODED ANIMALS COMPARED WITH THAT OF CURARIZED OR PITHED WARM-BLOODED ANIMALS.

Curve for Nutrition Laboratory tortoises represents only 5-kg. tortoises, on basis of flesh weight. Curve entitled "N. L. cold-blooded series" is curve for rattlesnakes, which is considered to represent, on the average, general trend of metabolism of all cold-blooded animals in Nutrition Laboratory series, except tortoises. Curve for Krogh's cold-blooded series is for small animals of from 9 to 35 grams. Data for Krogh's curarized dog are indicated by letter H, those for Velten's curarized rabbit by letter V, those for Krarup's pithed rabbit by letter K.

the generally demonstrated fact that the smaller the animal the greater the heat production per unit of body weight.

A similar comparison of these groups of animals has been made on the body-surface basis in figure 105. The same letters have been employed to designate the different warm-blooded animals as were used in figure 104. The body surface has been computed for the warm-blooded animals from the two-thirds power of the body weight and a K of 10. For Krogh's

small cold-blooded animals constants of 9 and 10 were used, and for the Nutrition Laboratory animals a constant of 12.5 for the snakes and of 10 for the tortoises (referred to the flesh weight). The scale for the ordinates in figure 105 represents an increase in heat production for each square of 100 calories per square meter of body surface or 10 times that shown in the preceding charts in this report for the metabolism per unit of surface area. Figure 105 shows perhaps more strikingly than does figure 104 that the metabolism of warm-blooded animals having, when under special conditions of operation or drugging, the same cell temperature as cold-blooded animals does not approximate in the slightest the metabolism of cold-blooded animals per unit of surface area. Specifically, the curarized dog of Krogh at  $14^{\circ}$  has a heat production per square meter of body surface of 150 calories, or about ten times that of the average cold-blooded animal at this same temperature. Krogh's dog at  $23^{\circ}$  and Velten's rabbit at  $26^{\circ}$  have a heat production agreeing reasonably well, averaging not far from 325 calories. But the cold-blooded animals at about  $25^{\circ}$  have an average heat production of approximately 45 calories. Krarup's pithed rabbit at  $26^{\circ}$  has a heat production of 169 calories, or about four times the average metabolism of the cold-blooded animals at this temperature. The great differences in the size of these animals should be taken into consideration in making these comparisons on the body-surface basis as well as those on the body-weight basis, that is, that Krogh's dog weighed about 950 grams, the rabbits about 2 kg., the cold-blooded animals of Krogh more nearly 30 or 35 grams, and the tortoises of the Nutrition Laboratory series 5 kg. (flesh weight about 3 kg.). For the cold-blooded animals of the Nutrition Laboratory series represented by the rattlesnake curve it would be difficult to state the exact average weight, but in any case it was much larger than that of any of the animals indicated in the upper part of the chart. It is possible that some of the discrepancies between the heat values for the cold-blooded and the warm-blooded animals may be accounted for by the great differences in size of the animals. On the other hand, Krogh's cold-blooded animals were all small in weight, 9 to 35 grams, and the cold-blooded animals in the Nutrition Laboratory series were all large in weight, 1 to 32 kg., and yet these two series of observations agree remarkably well on the body-surface basis.

In the comparisons made in figures 104 and 105 there is no indication of even an approximation to uniformity in the metabolism of warm-blooded and cold-blooded animals when the cell temperature is precisely the same. But it may be argued that warm-blooded animals subjected to curare or pithing are apt to die at these low cell temperatures, as the protocols of various observers have shown, and that the differences between the two types of animals may be explained by the abnormal condition of the warm-blooded animals. In answer to this criticism one has but to examine the heat values obtained, for example, at a fairly high temperature, that is, at  $30^{\circ}$ , which all animals withstand readily. The heat production of the three warm-blooded animals shown in figure 105 would average 470 calories per square meter of body surface per 24 hours at  $30^{\circ}$ . This is in striking contrast to the average metabolism of the cold-blooded animals

indicated by the three curves at the base of this chart, which would be not far from 60 calories. This difference in the metabolism even at 30° is of particular significance, since there is a recognized danger in cooling warm-blooded animals below 25° and there is likewise stated to be an equally great danger in heating cold-blooded animals above 30°. A cell temperature of 30° may therefore be considered to represent a middle or average point, against which the criticism can hardly be raised that it is too low for the curarized warm-blooded animal or too high for the cold-blooded animal. At this particular temperature the metabolism of the curarized or pithed warm-blooded animal per unit of surface area is eight times greater than that of cold-blooded animals at the same temperature.

#### COMPARISON OF METABOLISM OF COLD-BLOODED ANIMALS WITH THAT OF WARM-BLOODED HIBERNATING ANIMALS AT LOW CELL TEMPERATURES

The objection to the comparison of cold-blooded animals with warm-blooded animals that have been drugged or operated upon has already been pointed out, as well as Rubner's contention that the hibernating animal is the only wholly normal warm-blooded animal with a low temperature that can be compared with cold-blooded animals. Although the Nutrition Laboratory carried out metabolism investigations over a period of six years at the New York Zoological Park and sought carefully to find some animals that were hibernating, it did not succeed in measuring the metabolism of any hibernating animal. Indeed, it has been the experience at this park that none of their animals hibernate, with the possible occasional exception of the bear. Hence, in order to compare the hibernating animal with the cold-blooded animal, we must have recourse to the relatively few accurately determined observations recorded in the literature.<sup>1</sup> Of these we have selected the series considered by Rubner to be one of the best illustrations of such research, namely, the observations of Nagai<sup>2</sup> on the marmot. Our attention was called a number of years ago to the extraordinary series by Mareš<sup>3</sup> on hibernating marmots. His results have also been critically analyzed in connection with the present study.

#### A CRITIQUE OF EXPERIMENTS BY NAGAI ON THE MARMOT

The investigations on the hibernating marmot by Nagai deservedly warrant most careful consideration. Of particular significance is the fact that he was able to study the intermediary metabolism, a study that our own research emphasizes to be of greater importance than we at first thought. Certain of the data used in the following consideration of Nagai's experiments have been taken directly from his own report and others have been based upon the calculations of Rubner, who has analyzed Nagai's results

<sup>1</sup> As this report goes into page proof (December 28, 1931) there appears in the *Quarterly Review of Biology* (1931, **6**, p. 439) an unusually comprehensive article by G. E. Johnson entitled *Hibernation in Mammals*. It is impossible at this stage of our report to discuss this important paper, other than to call attention to the width of its scope and to the fact that it contains an extensive collection of references to the literature on hibernation. No new evidence on the respiratory exchange is, however, included.

<sup>2</sup> Nagai, H., *Zeitschr. f. allg. Physiol.*, 1909, **9**, p. 243.

<sup>3</sup> Mareš, F., *Bohemian Arch. Med.*, *Journ. Advancement Med. Sci.*, Prague, 1889, **2**, pp. 458-527; *ibid.*, *Compt. Rend. Soc. de Biol.*, 1892, 9th ser., **4**, p. 313.

in detail. Nagai made numerous experiments on two marmots in deep sleep and found that when the marmot's rectal temperature was  $10^{\circ}$ , the average oxygen consumption was 30.5 c.c., and the average carbon-dioxide production was 18.7 c.c. per kilogram of body weight per hour. In six experiments with the marmots in a normal condition, awake and at an average body temperature of  $36.5^{\circ}$ , the average oxygen consumption was 605.5 c.c. and the average carbon-dioxide production 486.9 c.c. per kilogram of body weight per hour. Ten observations with the marmots at an average rectal temperature of  $24.4^{\circ}$ , when "drunk with sleep," showed an oxygen consumption of 258.0 c.c. and a carbon-dioxide production of

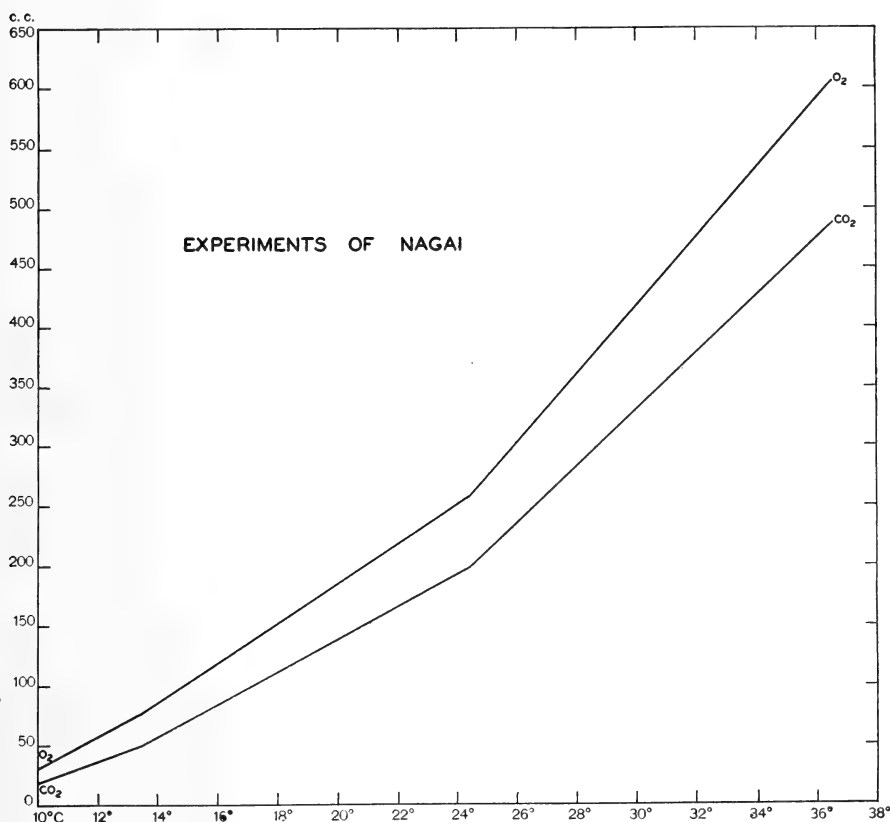


FIG. 106—OXYGEN CONSUMPTION AND CARBON-DIOXIDE PRODUCTION PER KILOGRAM OF BODY WEIGHT PER HOUR, REFERRED TO RECTAL TEMPERATURE—NAGAI'S MARMOTS, AWAKE AND HIBERNATING.

Ordinates represent cubic centimeters of oxygen and carbon dioxide. Marmots were in deep sleep at  $10^{\circ}$ , in light sleep at  $13.5^{\circ}$ , drowsy at  $24.4^{\circ}$ , and awake at  $36.5^{\circ}$ . These curves are reproduced from figure 6 in Nagai's article published in *Zeitschr. f. allg. Physiol.*, 1909, 9, p. 259.

199.8 c.c. Two observations on a marmot in light winter sleep, having an average rectal temperature of  $13.5^{\circ}$ , showed an oxygen consumption of 77.3 c.c. and a carbon-dioxide production of 50.0 c.c. per kilogram of body weight per hour. Nagai has embodied the results of these measurements in two curves, one for the oxygen consumption and one for the carbon-dioxide production, which are reproduced here in figure 106.

These two curves of Nagai are extraordinarily parallel when one considers the pronounced difference in the method of measurement of the oxygen consumption and the carbon-dioxide liberation. Furthermore these two gaseous factors undoubtedly represent different conditions with warm-blooded and cold-blooded animals. Thus, oxygen consumption in the case of the warm-blooded animal usually implies almost immediate oxidation and disengagement in the form of either water or carbon dioxide, and carbon-dioxide exhalation or liberation (except in instances of over or under ventilation) usually is a measure of the carbon-dioxide production. In the case of the cold-blooded animal, however, the oxygen consumption or absorption may not be an index of the actual oxidative processes prevailing at the moment, and the carbon-dioxide exhalation may be considerably different from the carbon-dioxide production. The unusual respiratory quotients found with cold-blooded animals at low temperatures hint at the difference in the gaseous exchange of the two great groups of animals. With rapidly rising or falling temperatures these adjustments between carbon-dioxide production and carbon-dioxide exhalation do not of necessity rapidly equalize, and in warming the cold-blooded animal rapidly to a higher temperature, for example, one may not necessarily assume that the metabolism measurement at the higher temperature represents the metabolism at that recorded temperature, owing to the possibility of a lag in the temperature adjustment. Indeed, it is generally recommended (and invariably was practised in our experiments) that cold-blooded animals should be maintained for a considerable time beforehand at the temperature at which they are to be measured. In experimenting with marmots, however, another factor comes into play that has not been generally experienced with cold-blooded animals. Thus, with rapidly changing temperatures, particularly rising temperatures and especially during the period of awakening, great differences in the temperature of the anterior and posterior parts of the marmot's body have been noted, and the rectal temperature has likewise been found to be lower than that of the mouth, at times many degrees below.<sup>1</sup> With these facts in mind one may argue instantly that the metabolism curves referred to body temperature presented by Nagai must be used only with considerable caution. For purposes of comparison, however, we have calculated the probable metabolism of Nagai's marmots at 16° based upon the following considerations. It is a fair question whether the rectal temperatures reported by Nagai as 24.4° and 13.5° represent the temperature of the whole animal or whether they present a false picture. But since, in general, Nagai's experiments were made over a relatively long period of time, at 24.4° being never less than three hours long and at 13.5° 1½ and 5 hours long, respectively, it is hardly probable that the rectal temperatures recorded by him were false. Little, if any, criticism can be raised against the series of measurements at 10° and, since these experiments lasted a long time, it is reasonable to suppose that the rectal temperatures recorded represent the true average cell temperature.

<sup>1</sup> Mareš, F., *loc. cit.* Du Bois, R., *Physiologie comparée de la marmotte*, Paris, 1896, pp. 119 *et seq.*

Direct heat measurements were out of the question,<sup>1</sup> and the heat production of Nagai's marmots at the low temperatures must therefore be calculated. The calculation may be made on several bases. The heat production may be computed from the oxygen consumption alone. This, however, requires a knowledge of the true caloric value of oxygen at the low respiratory quotients (averaging 0.61) obtained at the time the measurements at 10° were made. Another method is to compute it from the average carbon-dioxide production at 10°. Rubner has employed a third method, calculating the heat production from the carbon-dioxide production and computing the energy relations in the protein metabolism. The surface area of Nagai's marmots has been calculated by Rubner as corresponding to 596 square centimeters per kilogram of body weight, and the heat production at 10° Rubner states to be 47.5 calories per square meter of body surface per 24 hours. If the computation is based upon the average oxygen consumption at 10° of 30.5 c.c. per kilogram of body weight per hour and the caloric value of oxygen is assumed to be that at a respiratory quotient of 0.70, and if Rubner's value for surface area is used, the heat production per square meter of body surface per 24 hours will be found to be equal to 57.7 calories. If the heat production is computed from the average carbon-dioxide production of 18.7 c.c. per kilogram of body weight per hour, the caloric value of carbon dioxide at a respiratory quotient of 0.70 (that is, 6.7 calories per liter), and the surface area of 596 square centimeters per kilogram of body weight, it will be 50.5 calories per unit of surface area. The heat production at 10° may be calculated, therefore, to be 47.5, 57.7 or 50.5 calories, depending upon the method of computation employed. In other words, there may be a variability of 22 per cent in the results according to the method of calculation.

We are not, however, interested in the metabolism at 10° *per se*, for the comparisons of cold-blooded and warm-blooded animals have been made for the most part at 16°. The prediction of the probable metabolism at 16° from the metabolism measured at 10° may be made in several ways, as has already been discussed (pp. 445 to 447). Whatever may be the criticism as to the probability of inequality in body temperature or inaccuracy in the records of true body temperature at the intermediate temperatures of 13.5° and 24.4° studied by Nagai, there can be no criticism with regard to the measurement of the body temperatures at 10° and at 37°. If the percentage increment for heat production between 10° and 37° is computed, based upon Rubner's estimate of 47.5 calories per square meter of body surface per 24 hours at 10° and 1160 calories at 36.7°, one finds that the metabolism increased 88 per cent

<sup>1</sup>Nagai believes that abnormal metabolic processes and especially increased oxidation are, in the main, responsible for the low respiratory quotients during hibernation. Krogh (*The Respiratory Exchange of Animals and Man*, London, 1916, p. 128) states that "it is obvious that it would not be possible to calculate the heat production of hibernating animals from their respiratory exchange, and a comparison between direct calorimetric experiments and respiration experiments would be likely to furnish a clue to the nature of the processes taking place." We can most strongly advocate this contention of Krogh. Calorimetric experiments with hibernating animals are imperatively needed.



per degree rise in temperature between  $10^{\circ}$  and  $37^{\circ}$ . On the basis of this percentage increase, the metabolism at  $16^{\circ}$  would therefore be 297 calories. This calculation assumes that the increase in metabolism with increasing temperature is a straight-line relation. From Nagai's curves (fig. 106) it is clear that if one admits the probability of the accuracy of his measurements in the intermediate temperatures, the relationship between metabolism and temperature is not a straight-line function but definitely a curve. Hence it seems more logical to compute the metabolism at  $16^{\circ}$  either from the oxygen consumption or the carbon-dioxide production at  $16^{\circ}$ , as indicated on these curves. The respiratory quotient at or near  $16^{\circ}$  is low (Nagai found on the average 0.64 at  $13.5^{\circ}$ ), but the error in computing the heat production from the caloric value of oxygen or carbon dioxide at an assumed quotient of 0.70 is not of any moment. According to Nagai's curve, the oxygen consumption at  $16^{\circ}$  would be 120 c.c. per kilogram of body weight per hour. The caloric value of a liter of oxygen at a quotient of 0.70 would be 4.7 calories. The heat production based upon the oxygen consumption would therefore be 227 calories per square meter of body surface per 24 hours. If the calculation is based upon the carbon-dioxide production at  $16^{\circ}$  and this is taken from Nagai's curve to be 85 c.c. per kilogram of body weight per hour, the heat production per square meter of body surface per 24 hours would be 229 calories. Thus the computed heat production per unit of body surface at  $16^{\circ}$  is 297 calories if a straight-line relationship between metabolism and temperature is assumed to exist between  $10^{\circ}$  and  $37^{\circ}$ . It is 227 calories if computed from the oxygen curve given by Nagai, and 229 calories if computed from the carbon-dioxide curve. The lowest value, 227 calories, is so much greater than the values found with any of the cold-blooded animals measured at  $16^{\circ}$  that it is inconceivable that there is any similarity between the marmot's probable metabolism at  $16^{\circ}$  and that of cold-blooded animals at the same temperature.

Before concluding definitely that there is no similarity between the heat production of the hibernating marmot and that of cold-blooded animals of the same cell temperature, one should make the comparison also upon the basis of the metabolism per unit of body weight. In the Nutrition Laboratory series of cold-blooded animals there was not a great difference between the largest and the smallest animals in the heat production per kilogram of body weight, although there was a tendency for the larger animals to have a smaller heat production. Comparison of the heat production per kilogram of body weight of the Nutrition Laboratory series of animals weighing about 2 kg. or over with the data for Krogh's series of animals, weighing only about 30 grams (fig. 101) has shown that Krogh's smaller animals had a much greater metabolism on this basis than did our animals, whereas on the body-surface basis the two series of observations agreed with considerable regularity (fig. 102). According to Rubner's calculation of the metabolism of Nagai's marmots at  $10^{\circ}$ , the heat production per kilogram of body weight would be 2.87 calories. This value would lie close to any general curve that might be drawn through Krogh's data for *small* cold-blooded animals plotted in figure 101. Hence

at first sight one would think that this agreement established a close relationship between the two groups of animals. The effect of absolute size, however, has been discussed in connection with the data presented in table 117 (p. 455), in which a comparison was made of animals ranging in weight from the 2.5-gram stickleback of Rubner to the 53-kg. alligator of the Nutrition Laboratory series. It is clear from an examination of this table that, in general, the larger the animal the lower the heat production per kilogram of body weight. It is therefore illogical to compare the heat production per unit of weight of marmots such as those of Nagai, weighing on the average 3150 grams, with that of a group of animals weighing each about 30 grams, such as those in Krogh's series.

The cold-blooded animals studied by the Nutrition Laboratory were not measured at 10°. For comparison of Nagai's marmots with this series one could either calculate the metabolism of Nagai's marmots at 16° or project the Nutrition Laboratory curve down to 10° by the use of a  $Q_{10}$  derived from the curve. The simplest procedure is to compute the heat production of Nagai's marmots at 16°, based upon the average oxygen consumption or the average carbon-dioxide production at this temperature as indicated by the curves in figure 106. Such calculation shows that the heat production per kilogram of body weight per 24 hours at 16° would be about 13 calories, that is, twelve or thirteen times greater than that of the cold-blooded animals of an equivalent weight (about 3 kg.) whose metabolism data are recorded in table 117 (p. 455). Ordinarily a comparison of these animals on the basis of the metabolism per unit of weight would hardly be permissible, but in the attempt to establish a connection between warm-blooded and cold-blooded animals, since so little is known regarding the laws governing their heat production and heat loss, every available means of comparison should be carefully considered.

Neither on the basis of the heat production per square meter of body surface nor on the basis of that per kilogram of body weight does the metabolism of the hibernating marmot, specifically the marmots studied by Nagai weighing 3150 grams, compare with that of cold-blooded animals of approximately the same weight or of much smaller weights, when the cell temperatures are the same. The heat production of the hibernating marmot at a low body temperature is governed by laws of an entirely different nature from those controlling the heat production of the ordinary cold-blooded animals.

#### A CRITIQUE OF EXPERIMENTS BY MAREŠ ON THE MARMOT

A most elaborate series of measurements on hibernating animals during deep sleep was carried out by Mareš nearly 45 years ago, in the Physiological Institute of Professor Tomsa.<sup>1</sup> Mareš employed an extraordinarily

<sup>1</sup>Mareš, F., Bohemian Arch. Med., Journ. Advancement Med. Sci., Prague, 1889, 2, pp. 458-527 (In Bohemian). About eighteen pages of the original article were translated from Bohemian into German in 1914 through the kindness of Professor Fritz Verzár, then at Budapest, now (1931) at Basel. The importance of this particular section led to a subsequent arrangement to have the entire article translated into English by Miss B. A. Haderbolets at the Nutrition Laboratory in September 1915. A digest of his research has also been published by Mareš in Compt. Rend. Soc. de Biol., 1892, 9th ser., 4, p. 313.

well-conceived technique and had a fine realization of the pitfalls to be found in this kind of research and the necessity for exact control.<sup>1</sup> He reports a series of thirteen experiments at approximately 10° on marmots in deep sleep. Each experiment was about 24 hours in duration, and the average oxygen consumption per kilogram of body weight per hour was 0.052 gram. A number of marmots were used in this series, the average weight of which was 182 grams. In the calculation of the surface area of these marmots we have employed the formula  $S=9.1 \times w^{2/3}$  in which the K, 9.1, is the same as that which has been used for albino rats. The caloric value of oxygen has been taken to be 4.7 calories per liter at an assumed respiratory quotient of 0.70. On this basis the heat production per square meter of body surface per 24 hours has been calculated to be 25.6 calories at 10°. The difficulty of ascribing a suitable caloric value to the oxygen consumed is recognized in this calculation. Probably an even greater error would enter into the calculation from the carbon-dioxide production, which is also reported by Mareš. The respiratory quotients given by Mareš are low, as is commonly found with hibernating animals.

For comparison with the observations in deep sleep, Mareš also made an extensive series when the marmots were awake, that is, when they had a rectal temperature of 37°. The environmental temperature ranged from 6.7° to 21.0° C. From these experiments, which Mareš specifically states disregard the factors of food, activity, general regime and size, he finds that the oxygen consumption per kilogram of body weight per hour was 3.854 grams. In this series of experiments there were four instances when the oxygen consumption per kilogram of body weight per hour was under 3 grams. On the supposition that these more nearly represent the basal metabolism or at least the standard metabolism at the given environmental temperature, the results of these four experiments (May 23, June 22, July 2 and July 12) have been averaged and the average oxygen consumption per kilogram of body weight per hour has been found to be 2.688 grams at an average environmental temperature of 19.4°. The average body weight was 212 grams, and the body surface with K equal to 9.1 would be 324 square centimeters. The heat production per square meter of body surface per 24 hours (respiratory quotient assumed to be 0.70) has been calculated to be 1394 calories. An environmental temperature of 19.4°, however, is low for metabolism measurements on warm-blooded animals, certainly for dogs, guinea-pigs and albino rats, and probably is below the optimum temperature for the marmot when awake. It is possible that the true basal metabolism of the marmot under normal conditions, when awake, would be not far from the traditional 1000 to 1100 calories. The value of 1394 calories is, however, much higher than the value of 1000 or 1100 calories at 16°, the temperature at which most of these comparisons with warm-blooded animals on the body-surface basis have been made.

Since Mareš' marmots were measured in deep sleep at a rectal temperature of about 10°, it is desirable for purposes of comparison with

<sup>1</sup> The experiments of Horvath on the hibernating Ziesel (Centralbl. f. d. med. Wissensch., 1872, 10 Jhrg., pp. 706, 721, 737, and 865) were a great stimulus to Mareš and are cited by him *in extenso*.

measurements made on cold-blooded animals at  $16^{\circ}$  to compute the probable metabolism of these marmots at  $16^{\circ}$ . Mareš gives no measurements at intermediate temperatures between  $10^{\circ}$  and  $37^{\circ}$  corresponding to the temperatures of  $13.5^{\circ}$  and  $24.4^{\circ}$  at which observations were made by Nagai. Hence no curve can be drawn for either the oxygen consumption or the carbon-dioxide production referred to temperature. It is possible, however, to compute the probable metabolism of Mareš marmots at  $16^{\circ}$  by two methods. It can be assumed that the increase in metabolism with increasing temperature is a straight-line function between  $10^{\circ}$  and  $37^{\circ}$ , and the metabolism at  $10^{\circ}$  can be "corrected" to that at  $16^{\circ}$  on the basis of the percentage increase in metabolism per degree rise in temperature between  $10^{\circ}$  and  $37^{\circ}$ . A second method is to calculate the  $Q_{10}$  between  $10^{\circ}$  and  $20^{\circ}$ , as shown by the two curves published by Nagai for the oxygen consumption and the carbon-dioxide production of his marmots (fig. 106, p. 483), and apply this  $Q_{10}$  to the average heat value for Mareš' marmots at  $10^{\circ}$  to raise it to  $16^{\circ}$ . The increase in heat production from 25.6 calories per square meter of body surface at  $10^{\circ}$  to 1394 calories at  $37^{\circ}$  amounts to 198 per cent per degree rise in temperature. On this basis the calculated metabolism at  $16^{\circ}$  would be 330 calories per square meter of body surface. Judging from the general trend of all metabolism curves with relation to temperature, however, one may not logically assume that the relationship will be a straight-line function. Nagai's oxygen curve (see fig. 106, p. 483) shows a  $Q_{10}$  of 6.0 between  $10^{\circ}$  and  $20^{\circ}$  and his carbon-dioxide curve of 7.3. If the  $Q_{10}$  of 6.0 is used, the calculated heat production of Mareš' marmots at  $16^{\circ}$  would be 102 calories per square meter of body surface per 24 hours. The  $Q_{10}$  of 7.3 would give a much higher value. The value of 102 calories based upon the  $Q_{10}$  of 6.0 is only about one-third that based upon the percentage increment in metabolism between  $10^{\circ}$  and  $37^{\circ}$ , as shown by Mareš' data, and according to our experience thus far in these predictions, 102 calories is the more probable value. This heat production of 102 calories per square meter of body surface at  $16^{\circ}$  is much greater than that noted with any of the cold-blooded animals, the data for which have been incorporated in figure 102. By reference to table 117 (p. 455), in which the observations by earlier investigators on cold-blooded animals at  $16^{\circ}$  have been compared with the observations of the Nutrition Laboratory on cold-blooded animals at this same temperature, it can be seen that the highest value is 64 calories with the 600-gram frog of Krehl and Soetbeer, and that all the other values are much lower, most of them more nearly from 10 to 20 calories. None of these values approximate the 102 calories calculated for Mareš' marmots.

Nagai's 3-kg. marmots at  $16^{\circ}$  have been shown to have a probable heat production per unit of surface area of 227 calories or more than double the heat production (102 calories) of Mareš' 182-gram marmots. In view of this difference between the two series of hibernating marmots and in view of the fact that the heat values for both series on the body-surface basis are much above the values for the heat production per square meter of body surface of any of the cold-blooded animals at  $16^{\circ}$ , little is to be ex-

pected from a comparison on the basis of the heat production per kilogram of body weight. To complete the picture, however, such calculation has been made for Mareš' marmots. From the average oxygen consumption per kilogram of body weight per hour at 10°, that is, 0.052 gram, and from the caloric value of oxygen at an assumed respiratory quotient of 0.70, the heat production per kilogram of body weight per 24 hours has been computed to be 4.1 calories. Correction of this value to 16° by the use of a  $Q_{10}$  equal to 6.0 (derived from Nagai's oxygen curve for marmots) gives a heat production of 16.4 calories per kilogram of body weight. This is a metabolism twice as high as that, on the average, of Krogh's small (30-gram) cold-blooded animals at 16°, as will be seen from figure 101 (p. 466), and many times higher than that of the larger cold-blooded animals in the Nutrition Laboratory series. The only animals, whose metabolism data are listed in table 117, that approximate the marmots of Mareš in weight are the 135-gram (flesh weight) tortoise of Rubner and the 110-gram lizard of Krehl and Soetbeer. Rubner's tortoise had a heat production of 6.5 calories per kilogram of body weight at 16°. The lizard of Krehl and Soetbeer, however, had a high heat production of 12.0 calories, which is more nearly like that of Mareš' marmots. Here, therefore, in the single case of the lizard of Krehl and Soetbeer and the marmots of Mareš there is a fairly close agreement in the metabolism per kilogram of body weight of the cold-blooded and warm-blooded animals at 16° C. Analysis, however, of the value of 12 calories computed for the lizard of Krehl and Soetbeer is necessary. This lizard was measured at 25° and at 37°, and a straight-line relationship between metabolism and temperature was assumed in projecting the metabolism from 25° down to 16°. The assumption of a straight-line relationship between 25° and 37° may be reasonably justified, but it is highly improbable that this straight-line relationship continued down to a temperature as low as 16°. Indeed, if the curve for this lizard followed anything like the trend of the normal curves shown by the animals in the Nutrition Laboratory series, those in Krogh's series, and the marmots of Nagai, one would have expected with this lizard a metabolism at 16° higher than 12 calories, possibly approximating the 16 calories computed for Mareš' marmots. On the other hand, if the calculation on the basis of such a straight-line relationship is permitted and the computed value of 16 calories for the lizard of Krehl and Soetbeer is compared with the results per kilogram of body weight for all the other cold-blooded animals listed in table 117, it can be seen that the lizard now has the highest heat production of any animal in this series of its own weight or less, with the single exception of Rubner's small fish, the stickleback. In view of the other facts brought out in this comparison it is hardly probable that this close agreement between the computed heat production per kilogram of body weight of Mareš' marmots at 16° and the computed heat production of the lizard of Krehl and Soetbeer at 16° can be anything more than a coincidence, due possibly to the activity of the lizard. One great difficulty with an apparatus such as that employed by Krehl and Soetbeer would be the inability to see the animal inside and accurately note whether it was active. Another fact that should

be taken into consideration is that the marmots of Mareš weighed on the average 65 per cent more than the lizard of Krehl and Soetbeer (182 grams as compared with 110 grams). Since, in general, the larger animal has the smaller heat production per kilogram of body weight, one would expect on this basis alone to find a higher metabolism with the lizard than with the marmot. In selecting *individual* animals for comparisons of this kind there is always the danger of irregularities in the determinations. One need only refer to our charts for individual boas (figs. 41 to 44, pp. 159 to 168) to see the possibility of the variability in metabolism. Hence, although there does exist this one illustration of a warm-blooded hibernating animal that has a metabolism *per kilogram of body weight* comparable with that of a cold-blooded animal half its weight, it is highly probable that this agreement may not be interpreted as of any real biological significance.

It is clear that the heat production of Mareš' hibernating marmot computed per square meter of body surface at 16° is much greater than that of any of the cold-blooded animals at 16°, the data for which are shown in table 117 and in figure 102. Hence the studies of Nagai and Mareš justify the general conclusion that the metabolism of cold-blooded animals is governed by an entirely different set of conditions from those governing the metabolism of warm-blooded animals in a state of hibernation, whose cell temperature is essentially the same as that of the cold-blooded animals with which they are compared. This conclusion applies not only with reference to the heat production per square meter of body surface of animals of greatly different size but likewise with reference to the heat production per kilogram of body weight of animals of substantially the same size.

#### STUDIES OF HÁRI AND ASZÓDI ON SMALL HIBERNATING MAMMALS

The meticulous care with which all the researches were carried out in the Budapest laboratory by Tangl and subsequently by Hári and Aszódi warrants special consideration of experiments by the two latter investigators. Hári<sup>1</sup> studied the carbon-dioxide production and the oxygen consumption of bats awake and during hibernation. From his results we have computed the heat production, assuming a respiratory quotient of 0.71. We find that in the waking condition one of his bats produced 177 calories per kilogram of body weight per 24 hours. Other bats, while hibernating, produced 4.5 calories, or only 2.5 per cent of that of the bat awake. The bats weighed approximately the same as a normal mouse or frog would weigh. We may therefore compare Hári's results with those of Krogh on small toads and frogs. We have calculated that Krogh's decerebrated toad at 4.2° C. produced 0.56 calorie per kilogram of body weight per 24 hours, his narcotized frog at 4.2° C. produced 1.58 calories, his curarized frog at 6.0° produced 2.03 calories, and his normal frog at 6°, 1.58 calories. The rectal temperatures of Hári's bats were not determined, but the environmental temperature during the sleeping periods was about 3° C. It may be assumed that the rectal temperatures were not considerably above the room temperature of 3° C. Yet the metabolism of these hibernating bats was double that of Krogh's cold-blooded animals at about the same temperature.

<sup>1</sup> Hári, P., Arch. f. d. ges. Physiol., 1909, **130**, pp. 90 and 112.

In 1921 Aszódi<sup>1</sup> published data on rats and mice in a semi-stuporous condition, with rectal temperatures as low as 21° C. A comparison of the bat's metabolism with that of other animals on the basis of surface area is extremely problematical, owing to the uncertain value of the body-surface constant, K, for the bat and the difference of opinion as to whether the large area of the bat's wings should be included in the computation of the surface area.<sup>2</sup> For mice, however, the body-surface constant has been shown by recent critical analysis (unpublished) at the Nutrition Laboratory to be well established as 9.0. Using the lowest values for the oxygen consumption of Aszódi's normal mice, 15 hours after food, at a rectal temperature of about 37° C., we have computed the heat production per square meter of body surface on the basis of a K of 9.0 and an average respiratory quotient of 0.71. We find that on the average Aszódi's mice at 37° produced 686 calories per unit of surface area. Since Aszódi's data show that at 21° the metabolism of his mice was approximately one-fourth that under normal conditions, their basal heat production at this lower temperature would be approximately 170 calories per square meter of body surface. According to the metabolism curve in figure 103 (p. 472), the cold-blooded animal at 21° would have a heat production referred to the two-thirds power of the body weight times the constant 10 of only about 29 calories or 17 per cent of that of the mice at this same temperature.

#### GENERAL CONCLUSIONS REGARDING COMPARISON OF METABOLISM OF COLD-BLOODED ANIMALS WITH THAT OF WARM-BLOODED ANIMALS AT TEMPERATURES LOWER THAN 37° C.

A critical analysis of the metabolism measurements made by Krogh on the curarized dog, by Krarup on the pithed rabbit, and by Velten on the curarized rabbit has shown that at all stages of measurement between 15° and 37° the heat production per square meter of body surface of these animals was much greater than that of the small cold-blooded animals in Krogh's series or the larger cold-blooded animals in the Nutrition Laboratory series. When the comparison was made on the basis of the heat production per kilogram of body weight, it was seen that at one temperature, about 26°, Krarup's rabbit of nearly 3 kg. had a metabolism a little lower than the 30-gram cold-blooded animals studied by Krogh, that is, animals weighing only about one one-hundredth as much. But except for this one instance, no similarity was found between the metabolic processes of the warm-blooded animals immobilized by curare or by pithing and the cold-blooded animals. Comparison of the metabolism of the normal hibernating marmots of Nagai and Mareš with the metabolism of cold-blooded animals at a cell temperature of 16° likewise showed no similarity in the metabolism of the two types of animals, for the marmots had a heat

<sup>1</sup> Aszódi, Z., *Biochem. Zeitschr.*, 1921, **113**, p. 70.

<sup>2</sup> A body-surface constant or K for the bat (including wings) of 57.5 has been reported by A. O. de Almeida, B. de A. Fialho, and O.-B. de C. e Silva, *Compt. Rend. Soc. de Biol.*, 1926, **95**, p. 956.

production many times greater than that of the cold-blooded animals. Hence one can not conceive of a uniformity in the metabolic activity of warm-blooded and cold-blooded animals at cell temperatures lower than  $37^{\circ}$ , and the method of comparing cold-blooded animals with warm-blooded animals by bringing the cell temperature of the latter down to that of cold-blooded animals by drugs, by some operative procedure, or by hibernation has not shown any metabolic uniformity between these two types of animals. The next obvious method of comparison is to warm the cells of the cold-blooded animal to approximately the temperature of the normal warm-blooded animal and compare the metabolism of the two groups measured under these conditions. This basis of comparison will accordingly be considered in subsequent pages of this report (pp. 494 to 506).

#### COMPARISON OF METABOLISM OF HIBERNATING MARMOTS WITH THAT OF COLD-BLOODED ANIMALS AT TEMPERATURES NEAR $0^{\circ}$ C.

It is possible that as its cell temperature approaches  $0^{\circ}$ , the hibernating warm-blooded animal may reach a condition of torpor approximating suspended animation, and yet it is not inconceivable that at  $0^{\circ}$  or one or two degrees above  $0^{\circ}$  the metabolism of warm-blooded and cold-blooded animals may be exactly the same. To be sure, the metabolic activity of both groups may be so feeble and may so nearly approach complete cessation that it would be impossible to measure it with the techniques available at the present day. Yet it can not be denied that at an extremely low temperature the metabolic activity, even though extremely feeble, might be the same with both groups. At least, theoretically, this is a possibility that must be considered, a possibility that, without too great distortion, may be compared to the tendency for all chemical and physical processes to cease when approaching the absolute zero in temperature. One may question why our comparison of hibernating marmots with cold-blooded animals was made at  $16^{\circ}$  instead of at a much lower temperature. It is clear from the trends of the curves presented in this report and from the different measurements of metabolism reported for warm-blooded animals that, if the cell temperature of all the animals had closely approached  $0^{\circ}$ , the metabolism of the cold-blooded and the warm-blooded animals would have been essentially the same. If all the animals had been measured at  $0^{\circ}$  or at that temperature at which the body fluids would not be frozen, the metabolism measurements would probably have been of the same order of magnitude, but extremely low and very difficult of determination. There would still be an important difference between the two great groups of animals in that many, if not most, of the cold-blooded animals could recover and live a normal life, even after exposure to a temperature just above the freezing point of their body fluids, whereas warm-blooded animals, certainly those poisoned by curare, do not withstand a temperature much below  $14^{\circ}$  or  $15^{\circ}$ . It has been assumed that hibernating animals rarely have extremely low temperatures. Indeed, Pflüger<sup>1</sup> was certain that cold below a certain point acts as a stimulus for waking the animals. The

<sup>1</sup> Pflüger, E., *Arch. f. d. ges. Physiol.*, 1878, **18**, p. 372.



minimum temperature to which hibernating animals have been subjected and from which they have subsequently recovered has been noted in a number of instances. Horvath<sup>1</sup> concluded that hibernating animals could tolerate a cooling of their body to  $+1.8^{\circ}$  C. Mareš<sup>2</sup> reports three 24-hour experiments with one of his marmots in which the environmental temperature ranged between  $4^{\circ}$  and  $5^{\circ}$  C. The rectal temperature was not taken. The metabolism was measured during this time. On the fourth day the animal woke, and the metabolism was measured during the period of awakening. It is clear therefore that, although warm-blooded animals as a whole do not recover when severely cooled, hibernating animals have the specific capacity for withstanding intense cold and completely recovering their normal condition. Just what would be the lowest critical point at which these animals would again automatically warm themselves is not definitely known. The fact that fish and other lower animals have been reported by Pictet<sup>3</sup> and other investigators to have lived a normal life after having been completely frozen and then thawed out would suggest that cold-blooded animals at least could stand a lower temperature than  $1^{\circ}$  or thereabouts, noted as the minimum for hibernating animals.

If there is to be a comparison, however, of the metabolism of warm-blooded and cold-blooded animals, it can by no means be confined to the metabolism at one temperature, such as  $0^{\circ}$  or  $1^{\circ}$ . Acting upon the elaborate treatment given to this problem by Rubner, we have made our comparisons thus far chiefly at the temperature of  $16^{\circ}$ , since for one group of cold-blooded animals, fish at least, this is not far from the optimum temperature. It is probably below the optimum temperature for most of the large cold-blooded animals that we studied (see page 496). To more nearly approximate their optimum temperature, we measured the metabolism at many temperatures from  $15^{\circ}$  or  $16^{\circ}$  up. This explains why the Nutrition Laboratory series contains so few observations below  $14^{\circ}$ . Temperatures below this are distinctly not optimum for the large cold-blooded animals and are below the optimum for most fish, excepting species such as the trout and the salmon.

## COMPARISON OF METABOLISM OF WARM-BLOODED ANIMALS WITH THAT OF COLD-BLOODED ANIMALS, CELL TEMPERATURE OF WHICH HAS BEEN RAISED TO $37^{\circ}$ C.

In the discussion in the immediately preceding pages, in which the metabolism of cold-blooded animals has been compared with the metabolism of warm-blooded animals whose cell temperature has been lowered below  $37^{\circ}$ , it has been pointed out that the metabolism of all animals, both warm-blooded and cold-blooded, would tend to approach the same level, the

<sup>1</sup> Horvath, A., *Centralbl. f. d. med. Wissensch.*, 1872, 10 Jhrg., p. 865.

<sup>2</sup> Mareš, F., *loc. cit.*

<sup>3</sup> Pictet (see detailed reference in footnote 1, p. 11, of this report). A survey of Pictet's findings and further studies in this field of anabiosis are assured, owing to the recent announcement of a grant for this work. (*Science*, 1931, n.s., **73**, p. 478.)

nearer the temperature reached  $0^{\circ}$  or the freezing point of the body fluids. To be sure, most animals, whether cold-blooded or warm-blooded, would die when the body fluids were frozen and the metabolism measured just before death would be extremely low. But, *a priori*, it may be assumed that the nearer these two main groups of animals approach the point of death, the more nearly is their metabolism the same. At  $16^{\circ}$ , on the contrary, which is a temperature not at all abnormal for many cold-blooded animals, there is a great difference between the metabolism of the two types of animals. This difference in the case of the warm-blooded animal whose body temperature has been lowered by pithing or curare may be attributed not necessarily to a difference in the inherent nature of the animal itself, but to the fact that it is physiologically abnormal when drugged or pithed. The hibernating animal alone of the warm-blooded group can be said to exist under normal conditions when its cell temperature is below  $37^{\circ}$ . Since the hibernating animal is physiologically normal, there is no reason to believe that the comparison of its metabolism with that of cold-blooded animals at, for example,  $16^{\circ}$  is not legitimate. But there are relatively few observations on hibernating animals (those of Nagai and Mareš) that are suitable for such a comparison, and it is believed that conclusions derived from such comparison should be supplemented by more data for normal, warm-blooded, hibernating animals. A second method of comparison will therefore be employed that will permit of considering the basal metabolism observations on a larger number of warm-blooded animals. Thus, the average metabolism of all warm-blooded animals as a whole under the usual normal basal conditions will be compared with the standard metabolism of cold-blooded animals, the cell temperature of which has been raised to that of most warm-blooded animals, namely  $37^{\circ}$ .

Since it has been found that the lowering of the temperature of the warm-blooded animal much below its normal body temperature results almost invariably in the death of the animal, it may be questioned what are the dangers involved in raising the cell temperature of the cold-blooded animal to  $37^{\circ}$ . The warm-blooded animal rarely recovers when its body temperature, either by means of curare, some operative procedure, or by immersion in ice water, is lowered much below  $20^{\circ}$ . The striking exception is the hibernating animal, which normally has a low cell temperature during winter sleep and which apparently is able to withstand a temperature nearly as low as the cold-blooded animal, namely  $0^{\circ}$ , and yet subsequently make a complete recovery. Are there such conditions that obtain with cold-blooded animals which enable them to withstand  $37^{\circ}$  without permanent injury?

Most cold-blooded animals usually do not exist at a cell temperature of  $37^{\circ}$  C. Many of the cold-blooded animals in the tropics, however, must be able to live at or near  $37^{\circ}$ , and there is as yet no evidence to show that the metabolism of tropical cold-blooded animals at  $16^{\circ}$  is any different from that of cold-blooded animals from the temperate and arctic zones. It has been contended by many investigators, notably Krehl and Soetbeer and Rubner, that cold-blooded animals do not tolerate a temperature of

37°, that they are actually injured by being placed in such a temperature, their metabolic activity is altered, and hence abnormal results are obtained. On the other hand, Tigerstedt declares that it is doubtful whether measurements on cold-blooded animals at 16° or below throw much light upon the problems in comparative physiology. In his remarkable article on the production of heat, Tigerstedt emphasizes that animals at low temperatures do not have a complete irritability.<sup>1</sup> The Nutrition Laboratory, in organizing its research, devoted special consideration to the measurement of the metabolism of cold-blooded animals at the higher temperatures, and a large number of its experiments were made at 28° or above. These observations enable a comparison of the metabolism of the two different types of animals at 37°. But since the objection was raised against the comparison at the low temperatures that the warm-blooded animals were physiologically abnormal except in the case of hibernation, the objection may also be raised against this comparison at 37° that the cold-blooded animals are abnormal. Before the comparison at 37° is made, therefore, one must consider what is the optimum temperature for cold-blooded animals and whether they are damaged at 37°.

#### OPTIMUM TEMPERATURE FOR RESEARCH WITH COLD-BLOODED ANIMALS

The fact that the body temperature of the cold-blooded animal is so labile that it closely approximates the temperature of its environment, whether high or low, brings up the question as to what is the suitable or ideal temperature for studying the life processes of these animals. From the standpoint of the effect of temperature alone, obviously the greater the temperature range over which the metabolism of the cold-blooded animal is studied, the more complete will be the information secured regarding the temperature coefficient. The Nutrition Laboratory's observations on cold-blooded animals were limited to temperatures for the most part between 16° and 30°, although other investigators have subjected cold-blooded animals to very low temperatures without damage. In this temperature interval from 16° to 30° there must be some range of temperatures best adapted for the normal life of these animals. This may tentatively be termed the range of optimum temperature. Below and above this optimum range, experience has shown that cold-blooded animals, as a rule, fail to live a normal life. At the lower temperatures they become stuporous and rigid. At the higher temperatures they become flaccid and death ensues. With warm-blooded animals the optimum temperature for metabolism measurements has been considered usually to be that just at or above the critical temperature, that is, the temperature at which the chemical heat regulation no longer functions and at which the minimum or basal metabolism prevails. This critical temperature (environmental) varies considerably with the different warm-blooded animals. With albino rats and with doves and pigeons it is very near 28°, but with the well-protected sheep and the thickly feathered goose it may be much lower. Indeed, with sheep, the environmental temperature may be as low as 0°

<sup>1</sup> Tigerstedt, R., Winterstein's *Handb. d. vergl. Physiol.*, 1910-1914, **3** (Pt. 2), p. 82.

without having any effect upon the metabolism.<sup>1</sup> With cold-blooded animals one can not speak of a minimum or basal metabolism, but nevertheless one may properly ask what is the optimum cell temperature for life.

Most cold-blooded animals, such as frogs, snakes and alligators, certainly in the temperate zones have two major annual life phases, one during the winter when they exist in a state of hibernation or stupor, frequently buried in the ground. Under these conditions the optimum temperature would be that at which they could still live and not be permanently damaged by extreme cold, a temperature possibly not far from 0°. At this low temperature they would have a minimum metabolism, and hence the drafts upon their body reserves would be reduced to a minimum and they could better endure the long period of cold. The second phase of their life is that corresponding to the growing season of plants, when it is necessary for them to search for food, attack and devour their prey, and digest it. During this period they must live at a higher temperature, a temperature at which there will be a greater irritability of the neuro-muscular system and particularly greatly increased digestive activity. Some fish possess this irritability at an extraordinarily low temperature. Thus, Rubner has pointed out the lightning-like movements of some of the cold-water fish, such as the salmon and the trout, which at a temperature but a little over 0° are capable of extremely rapid movements. Other fish require a higher temperature, but experimenters in general have shown that fish do not withstand temperatures that are much above 25°.² Thus, Britton³ argues that fish withstand 25° with little difficulty but usually die at 30°, which is in full conformity with Rubner's belief. Probably the optimum temperature for most fish is not far from 10° to 15°. Among the reptiles and amphibians undoubtedly the environmental temperatures under which they live vary greatly according to their geographical location. In the temperate zone the hibernating snake, buried in the ground during the winter, has a much lower body temperature than any snakes in the subtropical or tropical zones ever approach, even at the period of lowest vital activity. It has been generally found, however, as a result of years of experience with cold-blooded animals in captivity in the various large reptile houses in the world, that snakes and other reptiles for the most part thrive best at a temperature of about 30° C. This temperature is materially higher than that found to be the optimum for fish, and hence it is a serious question whether metabolism measurements made on fish, on the one hand, and on reptiles and amphibians, on the other hand, at 15° or 16°, for example, are at all comparable. Striking evidence in favor of such comparison is furnished by the observations of Krogh with goldfish, frogs and toads, the metabolism of which at the lower temperatures was found to be

<sup>1</sup> Benedict, F. G., and E. G. Ritzman, *Wissensch. Arch. f. Landw., Abt. B., Tierernährung u. Tierzucht*, 1931, **5**, p. 57.

<sup>2</sup> In discussing the temperature at which animals can be normal, Rubner (*Biochem. Zeitschr.*, 1924, **148**, p. 284) comments on the fact that Maurel and Lagriffe (*Compt. Rend. Soc. de Biol.*, 1899, **51**, pp. 797, 875, and 915) give 30° to 32° as the maximal temperature for fish, which is higher than would be expected.

<sup>3</sup> Britton, S. W., *Amer. Journ. Physiol.*, 1924, **67**, p. 411; see, also, Britton's discussion on extreme hypothermia in various animals and in man, published in the *Canadian Med. Assoc. Journ.*, 1930, **22**, p. 257.

remarkably uniform (fig. 102, p. 467). It has been frequently noted, however, that at 15° or 16° these animals are in a semi-stuporous condition.<sup>1</sup> Thus, Regnault and Reiset found that at 7.3° their lizards were completely inert and at 14.8° they were only half awake.<sup>2</sup> Apparently the lower limit of irritability for their animals was reached at 15° or 16°. But whatever the lower limits of temperature favorable to life among the reptiles, greater interest from the standpoint of comparative physiology attaches to the question as to what are the upper limits of temperature suitable for cold-blooded animals.

Since 30° is the temperature commonly maintained in reptile houses, certainly this is not to be considered too high a temperature for reptiles. It is, however, too high for fish, and Rubner's experience has shown that it is too high for most frogs. Indeed, Rubner states that he has noted that some frogs at 30° remain for a long time flaccid and that many of them die, but that another species (*Rana mugiens*, for example) withstand 37°. His interpretation of this inequality is that there is a latency in the optimum irritability of the protoplasm through disuse, such as takes place when an animal lives for a long time at the lower temperatures.

Vernon states that the irritability of the snake's muscles is lost between 40° and 43.5°, that with land tortoises this irritability ceases between 42.5° and 52°, and with water turtles between 43.5° and 45.5°.<sup>3</sup> Battelli and Stern<sup>4</sup> found with insects that at temperatures above 45° the respiratory exchange began to decrease. Baldwin<sup>5</sup> is certain that with the turtle a temperature of from 39° to 41° for thirty minutes or more is dangerous, and he states that even at 27° these animals show signs of discomfort with rapid respiration. On the other hand, Richet<sup>6</sup> found that a tortoise heated in an oven at 38° to 39° lived for eight days. He concluded from this fact and from other observations on fish and insects that cold-blooded animals can live a long time at the high temperature of 40°. The majority of the observations by earlier investigators, however, give evidence that the higher temperatures are distinctly damaging to cold-blooded animals.<sup>7</sup>

In the observations made by the Nutrition Laboratory it was desired to increase the body temperature of the reptiles studied, until they approached as nearly as possible 37°, *i.e.*, the temperature of humans and other warm-blooded animals. It was soon found that it was impracticable to accept the record of environmental temperature as a true index of the temperature of the animal's cells, owing to the profound effect of the vaporization of water upon the body temperature of the cold-blooded animal. Consequently the rectal temperature of our animals was often de-

<sup>1</sup> Apparently cold-blooded animals may succumb to a lung infection as a result of cooling. See article on autopsy of a snake by Phisalix, *Compt. Rend.*, 1925, **180**, p. 471.

<sup>2</sup> Regnault, V., and J. Reiset, *Annales de Chim. et de Phys.*, 1849, 3d ser., **26**, p. 480.

<sup>3</sup> Vernon, H. M., *Journ. Physiol.*, 1899, **21**, p. 239.

<sup>4</sup> Battelli, F., and L. Stern, *Biochem. Zeitschr.*, 1913, **53**, p. 50.

<sup>5</sup> Baldwin, F. M., *Amer. Journ. Physiol.*, 1925, **72**, p. 210.

<sup>6</sup> Richet, Ch., *Revue Scientifique*, Paris, 1885, 3d ser., **9**, p. 202.

<sup>7</sup> From the work of Krüger (*Zeitschr. f. Morphol. u. Ökolog. d. Tiere*, Abt. A., 1931, **22**, p. 759) it is clear that cold-blooded animals, when sunning themselves, may rapidly reach temperatures of 40° C. or even above.

terminated, and with the 1931 python invariably determined. We succeeded in raising the temperature of a number of the snakes to  $37^{\circ}$ , and measuring their metabolism at this temperature. Some animals, notably the rattlesnakes, were brought to a temperature as high as  $44^{\circ}$  or  $46^{\circ}$ , in order to study them in what might be termed a condition of pyrexia, with the specific object of noting the trend of the metabolism above  $37^{\circ}$  as compared with that below  $37^{\circ}$  and of noting whether the percentage increase in metabolism or the  $Q_{10}$  would approximate that of man, for example, in fever. Our experiments with very high temperatures were limited to rattlesnakes, which could be replaced. All those heated above  $40^{\circ}$  subsequently died, but their metabolism measurements up to  $40^{\circ}$  and, indeed, up to  $46^{\circ}$  showed such a mathematical regularity in the general trend of the metabolism with the increasing temperature as to lead to the belief that in all probability the animals were not sufficiently damaged *at the time of measurement* at the high temperature to produce an abnormal metabolism. In these high temperature experiments there may be three evidences of damage. If the animal dies, it is certain that it was damaged, although, as just pointed out, it may not have been sufficiently damaged *at the moment of measurement* to affect its metabolism. If the animal becomes flaccid and motionless, it must be in an abnormal state, and metabolism measurements under these conditions must reflect this state. But perhaps the most accurate test of whether an animal has been damaged is to determine whether, after subjection to a high temperature, it recovers sufficiently so that its metabolism subsequently at a lower temperature corresponds to its metabolism measured at the same low temperature prior to the exposure to the high temperature. If the metabolism at the low temperature is the same both preceding and following the stay at the high temperature, this is proof that any possible damage incurred was only transitory and did not permanently affect the animal. These evidences of damage were carefully considered in the Nutrition Laboratory series of observations, particularly with the 1931 python.

Another indication that the cold-blooded animal is possibly approaching a damaging temperature is the trend of the metabolism with increasing temperatures. If, for example, above  $30^{\circ}$  the metabolism, instead of increasing according to the normal trend indicated by the majority of the curves such as were obtained with our cold-blooded animals, reaches a plateau and the curve flattens out, one could infer that a damaged state was being approached. Such a plateau was shown by boa C (figs. 43 and 57, pp. 161 and 226) the metabolism of which reached a plateau at a relatively low temperature. Likewise one of our tortoises (tortoise Z at about  $26^{\circ}$  to  $30^{\circ}$ ) gave a hint, but no more, of such a plateau. With the 1931 python, experiments were especially arranged to study this phase of the problem, the animal being subjected to a more or less continually increasing temperature in relatively dry air and the metabolism measured at these temperatures before it ever experienced  $37^{\circ}$ . The python was then studied at a rectal temperature of  $38.7^{\circ}$  and subsequently was measured again at lower temperatures, when the same results were obtained that had been secured before it was subjected to  $38^{\circ}$  (table 56, p. 211). It was then again meas-

ured at a rectal temperature of  $37.9^{\circ}$ , and subsequently at a much lower temperature. Again no hint of damage appeared. The python did not die, but was finally killed for autopsy. At the high temperatures it was by no means lifeless and flaccid. Indeed, after it had been twice at a rectal temperature of  $38^{\circ}$ , its tonicity was sufficient for it to make freely muscular contractions at different parts of its body, when held by the head suspended full length, as will be seen by the photograph in fig. 37 (p. 140), which was taken at the end of the entire series of observations on it and just before it was killed. Furthermore, the python on this last day demonstrated its activity and liveliness by savage attempts to bite those handling it (fig. 38, p. 141). Thus with this animal, after a number of experiments at temperatures around  $37^{\circ}$ , there was no hint of any damage whatsoever. As a matter of fact, this python was studied on one day with a rectal temperature of  $38.7^{\circ}$ , on another day with a rectal temperature of  $37.9^{\circ}$ , and on two other days with rectal temperatures of  $36^{\circ}$  (table 56, p. 211). Emphasis is laid here upon this fact, because the metabolism of this python as measured at  $37^{\circ}$  or over is not strikingly at variance with that noted with our rattlesnakes at  $37^{\circ}$ , and these observations give a fairly good indication as to the probable metabolism of large cold-blooded animals at this high temperature.

If the optimum temperature of cold-blooded animals other than fish and frogs is to be roughly estimated, one might say that it would probably be not far from  $28^{\circ}$  to  $30^{\circ}$ , certainly among the species of animals that were studied by the Nutrition Laboratory. Our rattlesnakes heated above  $40^{\circ}$  all died. Many warm-blooded animals likewise can not withstand temperatures much above  $37^{\circ}$ , although frequently there can be a transitory increase of at least  $5^{\circ}$  in their cell temperature without permanent damage. When one is comparing cold-blooded and warm-blooded animals, it is important to note that the damaging temperature at the higher limit is approximately the same, certainly for the protoplasm of the snake and the tortoise, as it is for the protoplasm of humans and most other warm-blooded animals. Only the birds bear normally such high temperatures as  $40^{\circ}$  to  $45^{\circ}$  C. The endurance at the high temperatures, however, seems to depend upon whether the air is dry or saturated. It may be argued, especially in view of the results obtained with our 1931 python, that it is physiologically permissible to subject a cold-blooded animal to a temperature of  $37^{\circ}$  in moderately dry air, particularly when one considers the prominent rôle that the vaporization of water plays in its heat loss, for under such conditions the animal's cell or rectal temperature is appreciably less than  $37^{\circ}$ . But since the cold-blooded animal's heat is almost wholly lost through the vaporization of water, it is doubtless physiologically unsound to subject these cold-blooded animals to a temperature of  $37^{\circ}$  in a saturated atmosphere. Warm-blooded animals find it difficult to endure  $37^{\circ}$  when the air is saturated. Relatively dry air was always used in the Nutrition Laboratory's experiments with cold-blooded animals. Dry air was likewise used by Rubner in his experiments with the tortoise. Krehl and Soetbeer, however, used saturated atmospheres. If one subjects the cold-blooded animal, at least of certain types, to an environmental tempera-

ture of 37° in dry or moderately dry air (thus permitting normal vaporization of water) and measures the metabolism under these conditions, this procedure can not, in our judgment, be considered as unphysiological when compared with the severe damage done to warm-blooded animals by curare, by cutting the spinal cord, or by plunging them into ice-cold water to lower their body temperature. It is true that at temperatures of 30° or below the likelihood of damage by existence in saturated air is remote, for the body temperature may easily be increased a fraction of a degree and the heat loss incidental to the normally low metabolism may proceed through radiation.

### BASIS OF COMPARISONS AT 37° C.

A number of the cold-blooded animals in the Nutrition Laboratory series, the so-called tropical animals (the pythons, the rattlesnakes and the boas) were warmed gradually to 37°, and their metabolism at this cell temperature was actually measured (table 120, p. 463). Other animals, especially the tortoises, the alligator, the lizards and the gopher snakes were not heated to 37°, and in these instances there are no actual measurements available for comparison. From a consideration of the course of the metabolism of our various species of animals with increasing temperature, as shown in the innumerable curves in the earlier portions of this report, it is evident that with all the different species the metabolism tends to increase with rising temperatures at a fairly definite rate. Furthermore, from the two metabolism curves definitely established by measurements with the pythons and the rattlesnakes at temperatures around 37° (see figs. 99 and 100, pp. 426 and 428), it can be seen that the course of the curves from 30° to 37° is a normal one. It is reasonable to conclude, therefore, that in the case of the other cold-blooded animals measured only as high as 30° or thereabouts, their metabolism curves may be legitimately projected to 37° by the method of inspection, on the assumption that the curve will have essentially the same trend found with the pythons and the rattlesnakes, and to conclude that this projection will indicate with a fairly high degree of accuracy the probable metabolism of these animals at 37°.

In the calculation of the probable metabolism of these cold-blooded animals by projecting the curves by the method of inspection it should be realized that at the higher temperatures cold-blooded animals become somewhat less quiet, and any activity whatsoever at the higher temperatures will give metabolism measurements that will tend to swing the curve upward more steeply. Hence the projection of curves based on such measurements will give a higher predicted metabolism at 37° than would be the case if the higher temperatures did not involve activity. These observations based on actual measurements and upon the predictions from the smoothed curves will be used as the basis for the following comparisons of the heat production of our cold-blooded animals at 37° with that of warm-blooded animals at their normal body temperature. These comparisons will be made with reference to the metabolism both per unit of body weight and per unit of body surface.



### METABOLISM PER UNIT OF BODY WEIGHT AT 37° C.

Inspection of the data given in table 120 (p. 463) shows that the values for the heat production per kilogram of body weight per 24 hours of our cold-blooded animals that were actually measured at about 37° range from 4.04 calories with the 1931 python to 14.65 calories with one of the rattlesnakes. Our smoothed curves for the rattlesnakes, pythons and boas that were measured at or near 37° show values varying from 5.9 to 7.7 calories (table 119, p. 462). With the cold-blooded animals studied by Krehl and Soetbeer, Martin, and Rubner (see also table 119), the heat production on this basis ranged from 9.6 to 36.0 calories.<sup>1</sup> If the smoothed curves for our tortoises shown in figure 99 (page 426) were projected to 37°, the probable metabolism would be about 7.5 calories per kilogram of flesh weight. It is conceivable that in the case of the lizards and the gopher snakes the heat production might possibly reach a value of 15 or 20 calories, although this is problematical, since the curves for these two species of animals are not as satisfactory as those for the other animals, being founded on too few experiments. Observations are needed with the gopher snakes and the lizards at 37° in a dry atmosphere, together with careful records of the rectal temperature, to show whether it is possible for animals of this type to reach a cell temperature of 37° and whether their heat-regulating mechanism is sufficiently well adjusted to the higher temperatures to allow the heat production to proceed at a standard rate. It has already been pointed out (p. 481) that in general cold-blooded animals at 30° have a lower heat production compared with that of warm-blooded animals, and it is interesting to note that at 37°, also, none of the animals in the Nutrition Laboratory series would have a metabolism approaching anywhere near that of warm-blooded animals, especially humans, except possibly the lizards.

### TOTAL METABOLISM AT 37° OF WARM-BLOODED AND COLD-BLOODED ANIMALS OF SAME SIZE

Owing to the great variability in the heat production of these cold-blooded animals per unit of weight at 37°, an average value for comparison with the average metabolism per unit of weight of different species of warm-blooded animals is not justifiable. Furthermore, the criticism may be raised against the comparison on the body-weight basis that, in most instances, these cold-blooded animals were much smaller than are many warm-blooded animals, such as man. It is permissible, however, to compare the heat production of our largest animals, such as the giant tortoises, the alligator, and the large python (which approach more nearly the weight of humans), with the metabolism values found with humans or other warm-blooded animals of the same body weight, and thus rule out the differences in size. According to the curve in figure 99, the pythons

<sup>1</sup>In comparing the metabolism of cold-blooded animals heated to 37° with the metabolism of warm-blooded animals, it is clear that further studies should be made of the metabolism of the echidna, which Wardlaw (Proc. Linnean Soc., New South Wales, 1918, 43, p. 849) has shown to have a temperature-regulating mechanism effective only while the body temperature lies between 27.6° and 32.6°. Outside these limits he states that the echidna behaves as a poikilothermic animal.

on the average would have a heat production at  $37^{\circ}$  of 5.9 calories per kilogram of body weight per 24 hours. Our 32-kg python, had it been measured at  $37^{\circ}$ , would therefore have a total heat production of 189 calories. According to the basal metabolism data for normal men published by Harris and Benedict,<sup>1</sup> a 24-year old man, weighing 33.2 kg. or much the same as this python, was found in three periods on one day to have a total heat production averaging 997 calories or somewhat over five times that of the python. If it is assumed that the metabolism of the 53-kg. alligator at  $37^{\circ}$  could be predicted from our curve for rattlesnakes in figure 99 (p. 426), its heat production at this temperature would be 7.7 calories per kilogram of body weight, or 408 total calories. In the list of basal data for normal men by Harris and Benedict there are three subjects (Nos. 82, 83, and 133) that weighed between 53.4 and 53.9 kg. Their total heat production on the average was 1470 calories, or 3.6 times the probable heat production of the 53-kg. alligator. Our 132-kg. tortoise (flesh weight 116.8 kg.) would have a probable heat production at  $37^{\circ}$ , according to the curve for all tortoises in figure 99, of 7.5 calories per kilogram of flesh weight or 876 total calories. The only man reported by Harris and Benedict as having a body weight approaching the flesh weight of this tortoise was subject No. 7, whose weight was 108.9 kg. In two periods on one day his total heat production averaged 2559 calories, or 2.9 times that of the giant tortoise. An 11.5-kg. dog has been reported by Lusk<sup>2</sup> to have had an average basal heat production over a period of 15 months of 16.2 calories per hour. This would mean a total heat production per 24 hours of 389 calories. In our cold-blooded groups the animal approaching most nearly the weight of this dog and which was measured at or above  $36^{\circ}$ , was our boa N, which weighed 10 kg. This boa had an actually measured total metabolism at  $36^{\circ}$  of 55 calories per 24 hours. The dog's metabolism was thus seven times greater than that of the boa of the same weight.

It is clear that the metabolism of the cold-blooded animal is of a different order from that of the warm-blooded animal. We are fully in accord with Tigerstedt in the belief that these two types of animals are of distinctly different natures and that there is no relation between them. Thus, Tigerstedt states:

"Der Unterschied zwischen den homoiothermen und den poikilothermen Tieren liegt also nicht allein in der Art und Weise, wie sich die Wärmebildung bei verschiedener äusserer Temperatur verhält bzw. in dem bei den Kaltblütern fehlenden Schutz gegen Wärmeverlust usw., sondern beruht ausserdem noch zum grossen Teil darauf, dass die poikilothermen Tiere selbst unter den günstigsten Umständen es nicht vermögen, auch nur annäherungsweise eine so grosse Wärmemenge zu bilden, wie dies bei den homoiothermen Tieren der Fall ist."<sup>3</sup>

Tigerstedt brings out clearly the idea that the cold-blooded animal can not produce the same amount of heat as the warm-blooded animal. We believe that under no conditions can the cold-blooded animal be

<sup>1</sup> Harris, J. A., and F. G. Benedict, Carnegie Inst. Wash. Pub. No. 279, 1919, table C, p. 43.

<sup>2</sup> Lusk, G., Science of Nutrition, 1928, 4th ed., p. 171.

<sup>3</sup> Tigerstedt, R., Winterstein's Handb. d. vergl. Physiol., 1910-1914, 3 (Pt. 2), p. 83.

warmed to the cell temperature of the warm-blooded animal and have a metabolism at all commensurate with that of warm-blooded animals of the same size, or indeed sizes much smaller.

#### METABOLISM PER UNIT OF SURFACE AREA AT 37° C.

The impracticability of comparing cold-blooded and warm-blooded animals on the basis of the heat production per kilogram of body weight has been sufficiently emphasized, and the method of avoiding this difficulty by comparing animals of essentially the same body weight in the two great groups has been pointed out. From our considerations thus far not only of our own material but notably of the values of Krogh, it can be seen that the heat production referred to the two-thirds power of the body weight or the surface area shows a much closer agreement between all the different cold-blooded animals than does the heat production per unit of weight. Seemingly, therefore, it would be justifiable to compare the heat production per square meter of surface area of a 10-kg. boa with that of a 50-kg. man, a 600-kg. steer or, indeed, any warm-blooded animal. This assumes that the surface-area law holds for cold-blooded as well as for warm-blooded animals, that is, that the heat production per unit of surface area of different cold-blooded animals varying greatly in weight is much the same throughout the entire cold-blooded series. It remains, therefore, to compare the heat production of cold-blooded animals at 37° with the heat production of warm-blooded animals per unit of surface area.

From our consideration of the data in table 119 (p. 462), we have assumed (based chiefly upon our own observations, but giving due consideration to the measurements of earlier investigators) that the average heat production of cold-blooded animals in general at 37° is 100 calories per square meter of body surface per 24 hours. In using this general average, which was derived for the most part from data for our animals actually measured at 37°, one might argue that the other cold-blooded animals in the Nutrition Laboratory series not measured at 37° should also be given consideration. Thus, the curve for gopher snakes in figure 100 (p. 428), if projected to higher temperatures as indicated by its present general trend, would certainly give a much higher value at 37° than 100 calories—probably 130 calories. The most aberrant curve is that for the lizards. It is conceivable that if the lizard curve were projected, it might indicate a value of 200 calories or more at 37°. The paucity of observations on lizards, however, has already been commented upon. The extension of the curve for the 5-kg. tortoises would strike the 37° line at just about 100 calories. The group of giant tortoises measured at or near 22° had a much higher metabolism than our other cold-blooded animals. If one were to consider their average metabolism at 22° as 85 calories per square meter of body surface and were to assume that their curve would have the same slope as that for the 5-kg. tortoises, their probable metabolism at 37° might be about 150 calories. These curves represent distinctly general slopes. Examination of the metabolism data (table 120, p. 463) for the individual animals measured at or near 37° (in the search for the highest

possible metabolism that could be found with a cold-blooded animal, if the body temperature was warmed to 37°) shows that there are a few instances when the heat production per unit of body surface was notably higher than 100 calories. One can conceive, therefore, that *some individual* animal might have a very high metabolism, if heated to 37°. But it is believed that the average heat production of cold-blooded animals in general at 37° is not far from 100 calories per square meter of body surface per 24 hours and, granting the possibility of the existence of individual animals with an aberrant or very high metabolism at 37°, we still feel justified in basing our comparisons with warm-blooded animals upon this average value.

It is commonly stated that warm-blooded animals at their ordinary cell temperature of 37° have a heat production from 800 to 1100 calories per square meter of body surface, depending upon the writer. Because of the well-known effect of environmental temperature upon warm-blooded animals and because many experiments with warm-blooded animals have been made at a temperature admittedly much below the critical temperature (frequently at 16°, when the critical temperature is nearer 28°), it can be assumed that 1100 calories represents, in general, the value at 16° and 800 calories more nearly that at the higher temperature where chemical heat regulation is ruled out.<sup>1</sup> With a single value of 800 calories for all warm-blooded animals at thermic neutrality we would have to disagree, for unpublished experiments of the Nutrition Laboratory show that the heat production per square meter of surface area ranges from approximately 600 calories with the albino rat and the dove to over 1700 calories with the horse. The variation in these values is two or three times greater than the range in the results for the different species of cold-blooded animals per square meter of surface area. Since, however, we are seeking the lowest metabolism of warm-blooded animals at 37° to compare with the highest metabolism of cold-blooded animals warmed to 37°, in order to discover how close it is possible to bring the metabolism of these two great groups of animals, we will assume that the *average* value for warm-blooded animals is 800 calories. The *average* value of 100 calories for all cold-blooded animals at 37° is only one-eighth of this value. If one is willing to concede that further experiments on a larger group of lizards at the higher temperatures would indicate (as does the trend of their curve projected to 37°) a heat production of about 250 calories per square meter of body surface, it can be seen that the warm-blooded animal would have a heat production over three times this highest conceivable value for cold-blooded animals at 37°.

On pages 502 to 503 comparisons were made between the total heat production of a single, large cold-blooded animal at 37° and the total heat production of a single human or of a dog of about the same weight. It was found that only in the comparison between the dog and the boa was the warm-blooded animal's metabolism as much as eight times that of the cold-blooded animal, as indicated by the comparison of the general

<sup>1</sup> Rubner (Sitzungsb. d. preuss. Akad. d. Wissensch., Phys.-Math. Kl., 1931, **17**, p. 313) assumes 1000 calories at 15° and 615 calories at 30°.

average values, 800 and 100 calories, for the metabolism per square meter of body surface of warm-blooded and cold-blooded animals, respectively. The 33-kg. man had a metabolism about five times greater than did the 32-kg. python, the 53-kg. men about four times greater than the 53-kg. alligator, and the very fat man about three times greater than the 132-kg. tortoise. These comparisons of *individual* animals should not be confused with the general comparison of 100 and 800 calories based upon the average *trend* of the metabolism of *all* animals. The metabolism of the 32-kg. python was not measured above 30° but had to be computed from the general curve for pythons. The human compared with this python was an unusually small man, whose metabolism was measured on only one day. Since this man and the python were of essentially the same body weight, it may be assumed that their surface areas computed from the formula  $S = K \times w^{2/3}$  would be the same. With the python  $K$  was taken as 12.5 and with man it was customary to accept the Meeh constant of 12.3. As a matter of fact, the Du Bois formula has shown considerable changes over the Meeh formula for humans, and a variation of 20 per cent or more in the actual surface area of these two animals may be expected, depending upon the method of computing the surface area. Thus, the comparison of average values per unit of surface area may not be expected necessarily to give the same result as that based upon individual values for total metabolism. The 53-kg. alligator was measured only at 19.5° and 22.1°, and its metabolism at 37° had to be predicted from the rattlesnake curve. This alligator, therefore, does not enter into the estimate of 100 calories per square meter of body surface for all cold-blooded animals. According to the Du Bois height-weight chart,<sup>1</sup> the 53-kg. men selected for comparison with the alligator would have a body surface averaging 1.6 square meters, varying somewhat with the height. The surface area of the alligator, computed from the two-thirds power of the body weight times the constant 12.6, has been estimated to be 1.8 square meters or somewhat over 10 per cent greater. With the giant tortoise there is the complication of how best to estimate the flesh weight, and the metabolism of this animal per square meter of body surface is so much higher than that of the other cold-blooded animals as to preclude including its data in any general average value. The fact, therefore, that in these individual instances, except for the dog and the boa, the total metabolism of the warm-blooded animal is only from three to about five times that of the cold-blooded animal of its same size instead of eight times greater (as shown by the comparison of the general average values per unit of surface area) is explained not only by the possibility of deviations from the average among individuals of a group but also by the possible differences in the computation of the body surface and the predictions of the metabolism at 37°. In any event, by no process of comparison can the heat production of a cold-blooded animal at 37° be found to amount to more than 34 per cent of the heat production of warm-blooded animals and for the most part it averages only about 12.5 per cent or in the ratio of 100 to 800.

<sup>1</sup> Du Bois, D., and E. F. Du Bois, Arch. Intern. Med., 1916, 17, p. 865.

## GENERAL CONCLUSIONS REGARDING COMPARISONS BETWEEN COLD-BLOODED AND WARM-BLOODED ANIMALS

In the preceding sections the actually measured metabolism of the cold-blooded animals in the Nutrition Laboratory series has been compared with observations on warm-blooded animals whose cell temperature has been lowered by artificial means and particularly by the more normal procedure of hibernation. When the body temperature of the warm-blooded animal is lowered by any of these means to between  $10^{\circ}$  and  $30^{\circ}$ , its metabolism is always much above the metabolism of cold-blooded animals measured at the same temperature, practically independent of size. This fact is shown with especial clearness when the comparisons are made on the surface area basis. It has likewise been demonstrated in a preceding section that cold-blooded animals of various sizes whose cell temperature has been raised to  $37^{\circ}$  have not been permanently damaged, and no inherent amount of latency in metabolic reaction to temperature has been introduced as a result of the transitions in temperature. Indeed, under these conditions the animals exhibited an increased metabolism at  $37^{\circ}$  perfectly in line with the curve projected from their other metabolism measurements at lower temperatures. The metabolism of the cold-blooded animals varies considerably at  $37^{\circ}$  per kilogram of body weight, depending upon the size of the animal, the larger animals in general having a much lower heat production per unit of weight than the smaller ones. The limits are, roughly speaking, from 6 to 11 calories per kilogram of body weight for cold-blooded animals weighing from 2 to 15 kg., up to 36 calories with animals as small as 110 grams. We have not found in the literature any records of cold-blooded animals with a smaller body weight that have been measured at  $37^{\circ}$  other than fish, but it is expected that the smaller the weight, the larger would be the heat production per kilogram of body weight, in accordance with this general trend. Hence it is difficult to compare directly any one average value for the heat production per kilogram of body weight of cold-blooded animals at  $37^{\circ}$  with any one average value for warm-blooded animals. The influence of size can perhaps best be eliminated by comparing the heat production per kilogram of body weight of warm-blooded and cold-blooded animals having approximately the same weight. A typical illustration has been given (p. 503) of a dog weighing 11.5 kg. that produced 34 calories per kilogram per 24 hours as compared with a 10-kg. boa that produced 5.5 calories. The most logical method of comparison, however, is that on the basis of the heat production per square meter of body surface. On this basis it is found that cold-blooded animals produce on the average 100 calories at  $37^{\circ}$ . Warm-blooded animals produce in general, if the lower value commonly ascribed to warm-blooded animals is accepted, 800 calories per square meter of body surface, or eight times as much. By any method of comparison, therefore, it is clearly seen that the cold-blooded animals when warmed to  $37^{\circ}$  have a metabolism only from one-third to one-eighth that of warm-blooded animals. This emphasizes again that the laws governing the heat production of cold blooded animals, even at  $37^{\circ}$ ,

are entirely different from those governing the heat production of warm-blooded animals at this temperature.

## POSSIBLE FACTORS EXPLAINING DIFFERENCE BETWEEN METABOLISM OF COLD-BLOODED AND WARM-BLOODED ANIMALS

From the experimental evidence presented in this report it is an indisputable fact that the metabolism both per kilogram of body weight and especially per square meter of body surface is much lower with cold-blooded than with warm-blooded animals at the same cell temperature, whether the cell temperature of the warm-blooded animal is lowered by curare, pithing, or hibernation to 16° or 10° for comparison with the cold-blooded animal or whether the cell temperature of the cold-blooded animal is brought to 37°, the normal body temperature of the warm-blooded animal. This finding would perhaps speak directly for a specific difference between the protoplasm of the cold-blooded animal and that of the warm-blooded animal. This difference in protoplasms is maintained to exist by Krehl and Soetbeer, but denied by Rubner. That the difference in metabolism can be entirely explained by any specific difference in the protoplasms alone is debatable, although such an explanation is perhaps the first that suggests itself.

It is conceivable that these two groups of animals may differ chemically or morphologically in a fundamental way. The possible chemical differences may first be considered, such as differences in the proportions of water, ash, fat and other supposedly metabolically inert matter in the body. Many of the cold-blooded animals, especially the lower pelagic animals,<sup>1</sup> have a much higher percentage of water in the body than does the average warm-blooded animal. Entirely aside from the extremes where the water content may be as high as 99.5 per cent,<sup>1</sup> cold-blooded animals such as those treated of in this report in general may be assumed to have a water content of about 80 per cent.<sup>2</sup> The body of the average warm-blooded animal has somewhat less water, averaging perhaps not far from 65 per cent.<sup>3</sup> Obviously with especially fattened animals, such as the

<sup>1</sup> Vernon (Journ. Physiol., 1895-96, **19**, p. 18) reports that transparent pelagic animals, such as the *Cestus* and the *Salpa pinnata*, contain only about 0.24 and 0.26 per cent solid matter in the body. The opaque or only slightly transparent littoral animals, such as the *Serranus* and the *Heliases*, contain about 20 per cent. The animals with the larger percentage of water had the lowest respiratory activity, and those with the lowest percentage of water the highest.

<sup>2</sup> Vernon (Journ. Physiol., 1895-96, **19**, p. 50) found 19.1 per cent solid matter in the skeletal muscle of frogs. Pütter (cited by Rubner, M., Biochem. Zeitschr., 1924, **148**, p. 232) found 21 per cent dry matter in the goldfish. Miescher (Miescher-Reusch, F., *Statistische und biologische Beiträge zur Kenntniss vom Leben des Rheinlaches im Süßwasser*, Internat. Fischerei-Ausstellung, in Berlin, 1880, p. 154; see also Miescher-Reusch, *Die histochemischen und physiologischen Arbeiten*, Leipzig, 1897, p. 166. Cited by Clark and Almy, Journ. Biol. Chem., 1918, **33**, p. 497, and by Rubner, Biochem. Zeitschr., 1924, **148**, p. 236) reports that the musculature of the salmon at the start of migration contains 34.6 per cent dry matter and at the end 21.8 per cent.

<sup>3</sup> Vernon (Journ. Physiol., 1895-96, **19**, p. 50) says mammalia are stated to contain about 30 per cent of solid constituents in their bodies.

domestic fattened steer or the Strasbourg goose, the percentage of water may be even less. Thus, Moulton reports the water content of a very fat ox to be 51 per cent.<sup>1</sup> A part, at least, of the higher metabolism of the warm-blooded animal may be due to the fact that there is a larger percentage of dry matter in the body and probably a larger percentage of active protoplasmic tissue.<sup>2</sup> But comparison of the water content of the body with cold-blooded and warm-blooded animals, 80 and 65 per cent, respectively, shows that only a part of the great difference in the metabolic levels of these two groups could be accounted for by differences in water content. Hence, even if the metabolism were expressed per kilogram of dry matter or per kilogram of dry matter raised by an exponent to some power of the dry weight, it would be impossible to wipe out any material amount of the large difference existing in the metabolic levels. Undoubtedly, therefore, some factor other than water content plays the most prominent rôle.

The proportion of the weight of the skeleton to the entire mass is likewise worthy of consideration. Although it has been argued that bone is far from being metabolically inactive, indeed, that bone marrow may be very active,<sup>3</sup> nevertheless bone is commonly considered to be more or less inactive. The percentage, therefore, of mineral matter in the total body of the animal may be considered as playing a rôle. Do the cold-blooded animals have a lower metabolism because there is a larger percentage of metabolically inert material in their bodies, such as water and possibly mineral matter, and in the case of the tortoise without doubt the horny shell? The amount of information with regard to the mineral matter in the complete body of the cold-blooded animal is meager. Rubner<sup>4</sup> has pointed out, based upon Inaba's analyses, that in the dry matter there is 15 per cent of ash in the fish, 7.6 per cent of ash in the frog, and 18 per cent of ash in the tortoise without shell. Our 1931 python contained 24 per cent of ash in its body (air-dry basis). The percentage of mineral matter in the body of the warm-blooded animal has been studied only in a general way, chiefly with domestic animals. Armsby<sup>5</sup> states that the total content of ash, including the skeleton, is approximately 7 per cent of the dry matter. It is thus obvious that with the cold-blooded animals there is a much larger proportion of metabolically inert ash, but this great ash content, even summed up with the greater water content, can account for only a part of the great difference between the metabolism of cold-blooded and warm-blooded animals.

<sup>1</sup> Moulton, C. R., *Journ. Biol. Chem.*, 1920, **43**, p. 67.

<sup>2</sup> The significance of dry matter in comparing the metabolism of animals of different species has been discussed most carefully by O. Cohnheim (*Zeitschr. f. physiol. Chem.*, 1901, **33**, p. 52), who has pointed out that medusæ may contain only 0.24 per cent dry matter. Cohnheim refers to Vernon's calculations of the metabolism per unit of dry substance and states that the highest values are found with the medusæ. The significance of surface area in the metabolism of these animals is given considerable weight by Cohnheim, chiefly on the basis of area as a receptive means of stimulation.

<sup>3</sup> McCrudden, F. H., *Arch. Intern. Med.*, 1910, **5**, p. 596; McCrudden, F. H., and H. Fales, *Arch. Intern. Med.*, 1912, **9**, p. 273; see also, McClendon, J. F., *Carnegie Inst. Wash. Pub. No. 252*, 1918, p. 250.

<sup>4</sup> Rubner, M., *Biochem. Zeitschr.*, 1924, **148**, pp. 225 et seq.

<sup>5</sup> Armsby, H. P., *The Nutrition of Farm Animals*, New York, 1917, p. 5.



It is conceivable that the proportion of metabolically inert fat and the melting point of the fat in the body may also be a differentiating factor in the metabolism of cold-blooded and warm-blooded animals. In the hibernating bear, for example, the fat has a low melting point. The thought arises that in the hibernating animal, fat with a low melting point may be an essential, so that when the cell temperature is greatly lowered there will not be a complete cessation of circulation caused by the solidification of fat. Does the fat in the body of the cold-blooded animal have a low melting point? When our 1931 python was dissected, buttons of fat were found in the body which, although the room temperature was about 21° or 22°, looked solid or semi-solid and certainly were not of a fluid nature. Does the fat in the body of all hibernating animals have a low melting point, and what is it? Why do not animals in a zoological park hibernate? It is common experience that they rarely hibernate. Is it because they are fed on food that results in the deposition of a fat with a high melting point? In the wild they may eat food producing a body fat having normally a low melting point. Fat with a high melting point would prevent hibernation, for at low temperatures the fat would solidify, clog the capillaries and kill the animal. In any further studies of the composition of the body of cold-blooded animals it is suggested that observations be included on the fat content, the melting point of the fat, the refractive index, the iodine number and the general distribution of fat in the body, and that these same observations be made with the hibernating animals.

Detailed analysis of the metabolically inert matter in warm-blooded animals would lead one not to include in the weight of active tissue such material as the horns and the hoofs of cattle, the feathers of birds and the fleece of sheep. It has recently been emphasized that the sheep's fleece may be possibly 12 per cent of its body weight.<sup>1</sup> If material that is metabolically inactive or that has a low metabolic activity is to be considered as not playing a rôle in the metabolism, it may be advisable to compute the metabolism data for all animals for comparison purposes on the basis of weight less inert matter. With the warm-blooded animal the inert matter other than water is a relatively small amount of the total body weight, such as horns, hoofs, feathers and fleece, but with some of the cold-blooded animals, notably the tortoise, a large percentage of the total body weight may be inert material. The weight of the tortoise shell has already been discussed (pages 355 to 362) and has been found to represent about one-third of the body weight. Probably the alligator's skin should also be considered metabolically inert.

The general conclusion to be drawn from this consideration of the possible chemical differences in these two main groups of animals is that, although chemical differences do exist, specifically although the water- and ash-content in the body may be greater among cold-blooded animals in general than among warm-blooded animals, nevertheless these chemical differences

<sup>1</sup> Benedict, F. G., and E. G. Ritzman, *Wissensch. Arch. f. Landw., Abt. B., Tierernährung u. Tierzucht*, 1931, 5, p. 43.

in the proportion of metabolically inert matter do not account appreciably for the great difference in the metabolism of these animals.<sup>1</sup>

The question then naturally arises as to whether this difference in metabolism exists because cold-blooded animals as a whole are of a different morphological structure from that of warm-blooded animals. The relationship between cause and effect in metabolic processes has been frequently discussed. It is known that when the metabolism increases, the heart rate and the body temperature increase. The question may be asked: Do the heart rate and the body temperature increase because the metabolism increases, or is the metabolism increased because the heart rate and the body temperature are increased? The changes in body temperature are usually very small with warm-blooded animals, but the change in heart rate may be great. For purposes of discussion one can conceive that the heart rate is an approximate measure of blood flow. The blood acts not only as an agent for the equalization of temperature throughout the body but as a carrier to the cells of three (if not more) important elements, each of which may participate in the metabolism. Thus, oxygen is borne to the tissues by the hemoglobin, nutrients (chiefly blood sugar but undoubtedly in part blood fat) are brought to the cells by the blood, and certain stimulating materials or hormones (thyroxin, for example) may be brought to the cells. When the heart rate is high, the body cells are bathed more frequently by these elements in the blood, and it is conceivable that the more frequently they are bathed with these three elements, the greater may be the metabolism. Consequently the relationship between blood flow and metabolism may be an important one. Measurements of blood flow, even under the most ideal conditions in the laboratory, are extremely difficult. One can assume that in general the blood flow is proportional to the heart rate, although this is far from a strict relationship. The heart rate of cold-blooded animals has been studied only too imperfectly. Our scattered data with the tortoise show that at the higher temperatures there are, to be sure, generally somewhat higher rates, but it is utterly inconceivable to compare the heart rate of a tortoise directly with that of a man or any other animal and assume that with the

<sup>1</sup> We are fully in accord with Rubner in his suggestion that in any further study of growth, knowledge is imperatively needed of the chemical constitution of the organism. We wish to express our profound admiration of the great work along this line of his scholar, Karl Thomas. According to Rubner (*Biochem. Zeitschr.*, 1924, **148**, p. 257), Thomas found that cats at birth contain 19.6 per cent dry matter, 20.3 per cent when the body weight is doubled, 26.2 per cent when it is doubled again, and 33.4 per cent when it is doubled still again. It is especially important to emphasize the study of Nagai on the marmot, who incorporated in his investigation extensive observations on the chemistry of the excreta. Since his studies were necessarily carried out with limited material and particularly by a procedure that has subsequently been superseded by improved technique, especially that of Folin, this important study instituted by Nagai should be furthered with modern methods. Nagai (*Zeitschr. f. allg. Physiol.*, 1909, **9**, p. 367) concludes from his results that the structural metabolism, or as he calls it the "Baustoffwechsel," continues during hibernation at much the same level as when the marmot is in the waking state. At least it is not depressed during hibernation to the extent to which the carbon-dioxide production and the oxygen consumption are depressed, and this points toward the stable character of the basic (not basal) metabolism. He likewise finds a relative constancy in the excretion of phosphates in hibernation and in the waking condition. These findings are all helpful in indicating future lines of study.

same rate the tissues are being supplied with proportionately the same amount of blood.

The relationship between the blood volume and the total body weight of animals has been studied for many years. The difficulties in its accurate measurement are great, for the amount of blood drained from the animal after killing is only a part of that existing in the body, the remaining portion of which is not easily removed. Indeed, the technique for such measurements is today under critical discussion. Even as concerns the human body there is a divergence of opinion as to what is the true relationship between the volume of blood and the total body weight, this relationship depending in large part upon the manner in which the blood is removed from the body and how completely it is removed. Little reliable information has been found in the literature regarding the supposed percentage of body weight existing as blood, owing to the imperfect technique.<sup>1</sup> The general picture, however, seems to be that the amount of blood in the cold-blooded animal is proportionately much smaller than that in the warm-blooded animal. The experience of the Nutrition Laboratory in the dissection of the large python (1931) strongly confirms this belief. At the time of dissection an astonishingly small amount of blood escaped from the animal, hardly enough to soil the hands of the operator or to soil the paper upon which the freshly opened animal was laid for photography and measurement. The heart, though beating, was (in the opinion of Dr. Rand) (p. 149) very small. No attempt was made to measure the amount of blood or to wash out the blood in the tissues, but it was evident that this 6-kg. animal had an incredibly small amount of blood.

There are several factors that may possibly serve as a stimulus to metabolism, one the structure of the animal itself, that is, the blood-vessels, the capillaries, and what one might call the "blood distribution area," which is small in white-fleshed animals such as the reptiles and liberal in the red-fleshed animals such as mammals. A second possible factor is the amount of blood present in the body to pass through the circulatory system. A third is the circulation or the amount of blood passing through the body per minute or, as one might say, passing through the heart per minute, although what passes through the heart may not be a true measure of what passes through the body, for there may be a "short circuiting" of the circulation with a relatively small passage of blood through the muscles. Finally, there is the composition of the blood itself. The composition of the blood would have to deal with the amount of hemoglobin, which determines the carrying power of the blood for oxygen, the percentage of blood sugar and fat, and the amount of hormones present. These four factors, structure of the muscles or the circulatory system, total amount of blood, volume output per minute, and composition of the blood all interplay.

The amount of oxygen carried to the cells is controlled by the amount of hemoglobin in the blood. The amount of nutrients carried to the cells would be determined by their percentage in the blood and thus the total amount circulating might be entirely independent of the total amount of

<sup>1</sup> A most careful consideration of this point has been given by Dreyer and Ray (Philos. Trans. Roy. Soc. London, *B*, 1910, **201**, p. 133; *ibid.*, 1911, **202**, p. 191).

blood. Similarly, the hormones might vary greatly, depending upon the actual amount present percentagewise in the total blood in the body. The determinations of the percentage amounts of these elements in the blood are relatively rare. Quincke<sup>1</sup> refers to an instance in which he found the hemoglobin of a hibernating marmot to be 64 per cent of the normal for blood and the red blood corpuscles 3.5 million or about 70 per cent of the normal. It is clear that measurements of the blood volume of cold-blooded animals are imperative and should be accompanied by a most careful study of the chemistry and the morphology of the blood, if this complicated problem is ultimately to be solved. Indeed, it is believed that the chemistry of the blood, particularly in its relation to the metabolism and its oxygen-carrying power, should be further studied along the lines so admirably instituted by Krogh and Leitch.<sup>2</sup>

From knowledge with regard to the total volume of the blood and its proportion of the total body weight, one can form an opinion as to the probable blood flow without direct measurements of the blood flow, measurements which in the cold-blooded animal may be extremely difficult. But it is believed that even with this knowledge regarding the blood flow, the differences in the metabolism of the warm-blooded and cold-blooded animals may not be explained, for there may be a relatively large volume of blood passing through the heart and yet the blood may be circulated only for a short distance through the body and the larger proportion of the body, particularly the extremities, may receive but a small supply of blood. It is therefore believed that the *distribution of the blood*<sup>3</sup> in the tissues may explain the difference in the metabolism of these animals. All the evidence strongly suggests that the cold-blooded animal has a relatively small blood flow and that its tissues are supplied with a meager volume of blood.<sup>4</sup> There are no large blood-vessels, and the flesh of such animals as the snake, the alligator and the fish exudes but little, if any, blood, when cut. It may be significant that those fish that are particularly active at very low temperatures, specifically the salmon and the trout, have a flesh distinctly rose colored. Is this coloration due to blood pigment, thus indicating a greater supply of blood to the tissues? It is clear that the metabolism

<sup>1</sup> Quincke, H., Arch. f. expt. Pathol. u. Pharm., 1882, **15**, p. 20.

<sup>2</sup> Krogh, A., and I. Leitch, Journ. Physiol., 1918-19, **52**, p. 288. Note also the Cornell University studies on the phosphorus content of the blood in fish and turtles (Science, 1931, n. s., **73**, No. 1889, Suppl., p. 14), the observations by F. H. Wiley and H. B. Lewis (Amer. Journ. Physiol., 1927, **81**, p. 692) on the nitrogen in the blood and urine of the turtle, and the report of D. B. Dill and H. T. Edwards (Journ. Biol. Chem., 1931, **90**, p. 515) on the physicochemical properties of crocodile blood.

<sup>3</sup> In the discussion by H. von Hoesslin (Arch. f. Physiol., 1888, p. 323) regarding the relation between size and metabolism, emphasis is laid upon the circulation rate per unit of weight. This, in our judgment, does not satisfactorily explain the situation. Undoubtedly the real factor is not the gross circulation rate but the circulation rate in the larger muscles or at least through the body tissues, where the greatest metabolism naturally occurs. Hence probably the expression "distribution of the blood" suggested above is better than the expression "circulation rate."

<sup>4</sup> In view of the great strength exhibited by the python, for example, in constricting its prey, one wonders how long this constriction or tonus could persist, if there is only a slow supply of oxygen and nutrients to its muscles. If the blood supply is feeble and these elements are quickly used, one can imagine that the constricting strength of the python might be of an explosive nature and could not endure long. On the other hand, it might be argued that by setting the muscles and holding them rigid, the snake is performing only static work and not effective muscular work as such.

of the trout and the salmon as compared with that of the white-fleshed fish should be most carefully studied.

Although it is still unknown whether increased blood flow is the result or the cause of increased metabolism, it may be concluded that where there is increased blood flow there is increased metabolism, and where there is meager blood flow there is a low metabolism.<sup>1</sup> This conclusion, coupled with the fact that the cold-blooded animals, such as we studied, have a relatively small amount of blood and that their muscles are not supplied with great blood-vessels, leads to the conviction that the explanation of the low metabolism of the cold-blooded animal is to be looked for not necessarily in a specific difference in the nature of the protoplasm but in a definite difference in the distribution of the blood carrying the three important elements, oxygen, nutrients, and hormones. Heat production is an internal factor. Heat loss is a surface factor. Heat production is determined by the blood supply to the tissues. Where there is a liberal blood supply to the tissues, the heat production *can* be high. Where the blood supply is low, it *must* be low. The snake with a large body weight and a small blood supply can not get to its tissues sufficient blood to increase its metabolism. On the other hand, the blood distribution is not determined by the metabolism, for with man the same blood distribution will permit his metabolism to be increased 1000 per cent.

It has been noted that the tortoises, both the 5-kg. and particularly the giant tortoises, had a higher metabolism per unit of surface area than did our other cold-blooded animals. Can this difference be explained by the fact that the tortoise, the flesh of which is distinctly red as compared with the white flesh of the snake, has a richer distribution of blood to the tissues than the other animals? But if this is so, why should the giant tortoises have a metabolism referred to surface area so much greater than the smaller tortoises? Why is not the metabolic level the same with both sizes of tortoise? It is not yet clear that even with a reasonably good blood distribution there will invariably be a sufficient supply of blood to enter these distributing areas. The blood volume of the tortoise and the volume output per minute may be of significance. The proportion of blood to flesh weight in the tortoise or the turtle is not known. The heart-rate values for tortoises, as determined by our electrocardiogram studies, undoubtedly are maximum rather than minimum, for the tortoises were almost continually in movement. It is well known, however, that normally the tortoise has a slow heart rate. It is thus highly probable that, although there may be a greater blood distribution in the case of this animal, the total amount passing through the system is, relatively speaking, small.

<sup>1</sup>Topper and Mulier (Arch. Intern. Med., 1928, **41**, p. 655) report metabolism observations on themselves when the leg was ligated. During the period when the circulation was cut off from the leg there was a pronounced lowering of the oxygen consumption, as measured on the Krogh apparatus. They state that their results are confirmatory of the findings of E. Helmreich (Zeitschr. f. d. ges. exp. Med., 1926, **53**, p. 578) who also studied the metabolism following ligation of an extremity. The experiments of Topper and Mulier were short, and the authors conservatively state that their results are merely suggestive of further work. It is significant, however, that these observations on humans indicate that even a temporary disturbance of blood distribution may have a pronounced influence upon the basal metabolism.

Throughout the entire discussion in this report the difficulty has been emphasized of computing the heat production of the tortoise for purposes of comparison, since such computations involve estimations as to the weight of shell and the surface area. The tortoise, therefore, differs from all the other cold-blooded animals we have studied in having a flesh with a much more liberal blood distribution and a large, heavy shell, which, although possibly a source for the vaporization of water, must obviously be of a less porous and moist nature than the skin of other reptiles. On the basis of the heat production per kilogram of body weight, the values for the large tortoises agree with those for the smaller tortoises. In the discussion of figure 98 (p. 398), in which the heat production per square meter of body surface per 24 hours of all the tortoises is referred to temperature, it was pointed out that there is a wide distribution of the plotted values, especially for the giant tortoises, and that the temperature relationship is a straight-line function rather than the well-known curve. It would appear, therefore, as if the tortoises presented throughout the entire study a wholly unusual condition. The highest degree of accuracy can be expected in the measurements of tortoises Y and Z studied at the Nutrition Laboratory in 1930, for these animals were more carefully controlled and observed over a much longer period than were the tortoises in the earlier series. In general, any error in measurement is evidenced by a higher rather than a lower metabolism, chiefly due to activity. It is still debatable whether the giant tortoises had the same degree of muscular repose as the small tortoises. In spite of our graphic registrations of activity, the conditions under which these large tortoises were measured were by no means as controllable as were those with the smaller tortoises. If the tortoise curve were to be based solely upon the observations with tortoises Y and Z, it would be measurably higher than that shown in figure 98. This would accentuate the difference noted throughout all the comparison charts, showing that the tortoises have a consistently higher metabolism than the other cold-blooded animals per unit of surface area.

It is more than possible that the difference in the blood distribution of the tortoise accounts for its generally higher metabolism. That its metabolism at 37° is not as high as that of warm-blooded animals at 37°, in spite of the richer blood distribution to the muscles, may be accounted for by the relatively small blood volume passing through the distributing areas. It would appear, therefore, as if the tortoise would occupy an intermediary position<sup>1</sup> between cold-blooded animals such as snakes, lizards, and alligators, and warm-blooded animals.

The mechanism by which the incubating python increases its heat production is not at all understood. It would seem to be impossible for the python to make any significant change in the vascularity of its blood-distributing system, with the possible exception of a slight distention of the peripheral vessels, although these are few. Hence the increased heat production of the incubating python must be due entirely to increased blood

<sup>1</sup> This is in full conformity with the experience of Dr. R. G. Hoskins of the Harvard Medical School, who finds that the muscle of the turtle is much nearer in its general physiological properties to the mammalian muscle than to the muscles of the other well-known cold-blooded laboratory animals.

flow. The measurement of even the heart rate of the python, incubating or non-incubating, presents a problem that we have not considered at all feasible. But it is clear that not only the tortoise but the incubating python represents a step in the development from a poikilotherm to a homoiotherm.

The significance of blood circulation or local distribution of blood in the hibernating animal is most interestingly discussed by Mareš.<sup>1</sup> He points out that Horvath<sup>2</sup> and Quincke<sup>3</sup> agree in supposing that the circulation of the blood in the hind part of the body of the hibernating animal is actually stopped, and that Valentine assumes that the circulation is weak on account of the greatly decreased activity of the heart. Mareš himself injected indigotin into the blood of the marmot in winter sleep. He had formerly observed that indigotin injected into the blood of winter frogs is not discharged by the liver as in the case of summer frogs, but remains in the blood and fills the blood capillaries in the liver, so that a natural injection appears. He expected to find much the same thing in the marmot in winter sleep, since he had discovered that under normal conditions of activity indigotin thus injected into the marmot was excreted quickly by the kidneys. In January 1887, 5 c.c. of a saturated solution of indigotin was injected into the jugular vein of a Casan marmot in hibernation. The mucous membranes in the head began to grow blue in a few minutes, and the skin on the front half of the body became distinctly blue, but there was no change in the color of the skin on the back part of the body. Fifteen minutes after the indigotin was injected, the liver, lungs and kidneys were quickly removed and placed in absolute alcohol. When the abdominal cavity was opened, the viscera appeared pale. The intestines, kidneys and bladder were altogether devoid of color. Microscopically it was impossible to find even a trace of coloring matter in the kidneys, but there was an abundance of it in the capillaries of the lungs and the liver. These studies indicate that, although there may be a liberal distribution of blood around the central part of the hibernating marmot, there is a small distribution in the large muscles and on the periphery of the body. Coincident with this condition is the low metabolism of the hibernating marmot.

Mareš' observations with indigotin suggest that a study of the distribution of the blood in cold-blooded animals might be made by noting the distribution of coloring matter injected into the veins and arteries. Would such injection show an extremely defective impregnation of the tissues, particularly the muscles, with coloring matter in the case of the cold-blooded animals and thus indicate a much less complete distribution of the blood through the large muscles than in the case of warm-blooded animals? Certainly modern studies in "Vitalfarbung" should be suggestive of methods.

It is clear that studies of the temperature in different parts of the marmot, both in the sleeping condition and particularly in the waking condition, are also important. These studies might represent a topographical

<sup>1</sup> Mareš, F., Bohemian Arch. Med., Journ. Advancement Med. Sci., Prague, 1889, **2**, p. 458.

<sup>2</sup> Horvath, A., Centralbl. f. med. Wissensch., 1872, 10 Jhrg., pp. 706, 721, 737 and 865.

<sup>3</sup> Quincke, H., Arch. f. expt. Pathol. u. Pharm., 1882, **15**, p. 1.

survey of temperature, such as was reported by Quincke in 1882,<sup>1</sup> but with the use of more modern thermo-electric needles. Any information with regard to the marmot in its various stages of winter sleep, particularly with relation to the blood flow and the blood supplied to the various tissues, must contribute toward solving this question of the connection between warm-blooded and cold-blooded animals. It is likewise clear that all animals on the border line between warm-blooded and cold-blooded animals, such as the echidna of Australia so interestingly studied by Martin<sup>2</sup> and Wardlaw,<sup>3</sup> would furnish especially fruitful fields for the furtherance of knowledge regarding this problem.

All these considerations lead to the conclusion that the distribution of the blood is the dominant factor in metabolism and that the higher metabolism of the warm-blooded animals may be explained by the fact that in their case there is a better distribution of the blood to the outer tissues and the peripheries. In order for the supposedly poorer distribution of the blood of the cold-blooded animal to be bettered, profound structural changes would be necessary. Hence it would seem as if the transformation of the cold-blooded animal into a warm-blooded animal would involve great morphological changes and not a relatively simple development of a chemical heat regulation or the development of peripheral phenomena dealing with the loss or conservation of heat.

The great aid to human physiology, pathology, and medicine that has been derived from observations on the lower warm-blooded animals is universally admitted, but the possibility of the better interpretation of human physiology and pathology by means of observations on cold-blooded animals has been only tardily recognized. The indispensable laboratory frog in elementary studies in physiology must now be supplemented by other and preferably larger cold-blooded animals. If our research serves no more than to point out to students in comparative physiology some of the intermediary phases that may occur between the lowest of the cold-blooded organisms and the highest of the warm-blooded organisms (man), it has been worth while.

## ACKNOWLEDGMENTS

In addition to the invaluable services rendered in the experimental side of this research by Mr. E. L. Fox and Mr. Colbert Mason, whose names are frequently mentioned throughout this report, we have cited also our obligation to Dr. Raymond L. Ditmars and to other staff members of the New York Zoological Park for their kind cooperation. The experi-

<sup>1</sup>The debt that physiology owes to the physician for his interest in physiological problems has already been pointed out in references to the classic study of Krehl and Soetbeer. It should also be noted that H. Quincke, when in medical service in Berne, became much interested in the temperature variations in the marmot. His measurements (*Arch. f. expt. Pathol. u. Pharm.*, 1882, **15**, p. 1) deal exclusively with the body temperature, with some observations on the blood, and indicate even at this early stage a concern in this important problem.

<sup>2</sup>Martin, C. J., *Philos. Trans.*, B, 1903, **195**, p. 1; *ibid.*, *Lancet*, 1930, pp. 561, 617, and 673.

<sup>3</sup>Wardlaw, H. S. H., *Proc. Linnean Soc. New South Wales*, 1918, **43**, p. 844.



ments at the Nutrition Laboratory in Boston were carried out by the technician responsible for most of the New York measurements, Mr. E. L. Fox, who was assisted by Mr. Basil James.

In this research, which extended, with interruptions, over 15 years, a large number of people were occupied in the elaboration of the experimental data for publication. Mr. W. H. Leslie had charge of the original calculations and tabulations and was aided by Miss Clara E. Borden. In the most active phases of the preparation of this report for publication the calculating, tabulating, typing, as well as the editing were all in the hands of Miss Elsie A. Wilson, secretary to the Nutrition Laboratory. Without her indefatigable efforts and care in handling the material it would have been difficult to have prepared this report for publication. In her work she was ably assisted by the Misses A. G. Harrington, A. Vuilleumier, E. Gundal, A. Swasey and H. Bulson.

Dr. Thorne M. Carpenter of the Nutrition Laboratory generously gave much of his valuable time to read especially the latter portion of the report. His most helpful and constructive criticisms have been deeply appreciated. Dr. Ditmars, in addition to his helpful responses to innumerable questions and requests for advice, has likewise read the entire manuscript.

The subject index of this book was prepared by Mrs. Cornelia Golay Benedict, who volunteered her services and devoted countless hours to make it as complete as possible.

#### ADDENDUM

As this manuscript goes to press, our attention is called to the most interesting article of A. B. Keys in the *Biological Bulletin of the Marine Biological Laboratory at Woods Hole, Massachusetts* (published October 1930, volume LIX, page 187). Keys describes a method of studying the gaseous exchange of aquatic animals and reports metabolism measurements on fish (without narcotic) ranging in weight from 4.3 to 257 grams. The environmental temperatures were from 16.7° to 20° C. Calculation of the heat production of these fish per square meter of body surface per 24 hours, based upon Keys' oxygen figures, a respiratory quotient of 0.72, and a body-surface constant of 10, and correcting all the results to 16° C., gives an average value for fish extraordinarily close to that reported by Rubner (*Biochem. Zeitschr.*, 1924, 148, p. 284) for fish.

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